Dispersal of Homo sapiens around the Indian Ocean rim: a geometric morphometric study of craniofacial diversity.

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Abstract

This thesis explores craniofacial diversity found in *Homo sapiens* around the Indian Ocean rim. Three dimensional landmark data, taken directly from the craniofacial skeleton, are examined in relation to the hypothesised southern dispersal route taken by *Homo sapiens* out of Africa during the Late Pleistocene. The thesis explores whether traces of this dispersal event are evident in the craniofacial morphology of modern human populations. It also explores further causes of morphological diversity between the populations.

The first part of the thesis examines the patterns of craniofacial diversity found in samples from around the Indian Ocean rim. Biological and geographical distances are correlated and the results show that geography plays an important role in determining observed patterns of diversity. Distance from Africa is found to be statistically significant, suggesting that traces of the original Late Pleistocene dispersal remain today. Having determined geography as important in creating craniofacial diversity, the thesis additionally explores other potential causes of morphological variation. The results find that environmental conditions, including temperature and rainfall, are correlated with craniofacial shape.

One finding of this initial section of the study is that there is considerable regional clustering of morphology in the samples from around the Indian Ocean rim. The second part of the thesis therefore examines dispersals within the identified regional clusters, including South and Southeast Asia, Melanesia and Australia. Craniofacial morphology is discussed in relation to proposed models of origin and evolution within these regions. Additionally, craniofacial variation within Polynesia is explored to provide a comparison of how diversity can develop over a relatively short period of time. The thesis concludes with a discussion of how craniofacial diversity is the result of a combination of multiple small founder effects and adaptation to local environmental conditions.

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Chapter 1

Introduction and Background

1.1 Introduction and objectives of thesis

The use of cranial data for reconstructing human evolution has a long history in biological anthropology (e.g. Howells, 1989, 1995; Lahr, 1996; Pietrusewsky, 2000). Many of these studies have been conducted on traditional metric and non metric traits and have looked at variation between and within populations (Larsen, 1997). The difference in precision and repeatability of measurement techniques, the conservative nature of variation, the direct link with the past and the demonstration of a genetic component (Sjøvold, 1984) are responsible for this continued interest.

As is the case in much of the previous research (e.g. Howells, 1989, 1995; Lahr, 1996), the present study will approach craniofacial variation in relation to a specific theory of human evolution. The southern dispersal route hypothesis (Stringer, 2000) is integral to the Recent African Origin model of human evolution and the present study will address this issue by exploring patterns of diversity found in populations from this proposed migration. This work forms part of a wider project exploring the evolution and dispersal of *Homo sapiens* around the Indian Ocean rim. One aim of the project is to highlight the importance of museum skeletal collections to studies of human evolution and thus only specimens taken from recent populations have been included in the study.

1.2 Structure of the thesis

The relevant literature to the overall topic is reviewed in the present chapter. An introduction to the general theories regarding the origins of *Homo sapiens* is given in Section 1.3.1 while specific theories of migration in particular regions are summarised in each results chapter. Sections 1.3.2 - 1.3.4 discuss the Late Pleistocene dispersal from Africa, with particular emphasis on the southern route hypothesis. Section 1.4 discusses further human dispersals in the various regions covered by the southern route hypothesis, for example Southeast Asia, and discusses some of the issues relevant to

these migrations. In Section 1.5 the biological effects of human dispersal are evaluated, looking at how genetics and morphology have been used to address this issue. Sections 1.5.4 and 1.5.5 discuss the effects of environment on the craniofacial skeleton, both in terms of the physical environment such as climate and the localised environment, for example diet. The materials and methods used in the thesis are covered in Chapter 2. Chapter 3 explores the patterns of craniofacial diversity found in population samples located around the Indian Ocean rim and tests hypotheses relating to the effects of geography on the patterns determined. In particular the patterns of diversity are tested in relation to the Out of Africa hypothesis and compared to results from genetic research. The effects of geography and climatic factors on craniofacial shape are assessed in Chapter 4. Chapters 5 and 6 explore the patterns of diversity found within regional groupings along the proposed dispersal route, those of South and Southeast Asia; and Melanesia and Australia respectively. In Chapter 7 craniofacial patterns of diversity beyond the Indian Ocean rim are discussed in relation to the settlement of Polynesia. The findings of the previous chapters are synthesised in Chapter 8 and conclusions regarding the determination of present day patterns of human craniofacial variation are presented.

1.3 Introduction to modern human origins

Although a single African origin is today widely accepted, the origins and evolution of *Homo sapiens* have led to major palaeoanthropological debate. The two main theories leading the discussions are the Multiregional and the Out of Africa hypotheses. The Multiregional model of human evolution proposes that there was no single geographic origin for all modern humans (Wolpoff *et al.*, 2000). It is believed that since the radiation of *Homo erectus* from Africa around 1.8 million years ago, a continuous transition has occurred from *Homo erectus* to *Homo sapiens*. The dispersed archaic human populations gradually evolved into modern *Homo sapiens* in different geographic areas with speciation prevented by extensive gene flow between the regions (Thorne and Wolpoff, 1992). Proponents of this model are keen to stress that multiregional does not mean independent multiple origins (Wolpoff *et al.*, 2000). Rather the underlying hypothesis is that a worldwide network of genic exchanges, between evolving human

populations that continually divide and reticulate, provides a framework of population interconnections that allows species wide evolutionary change (Wolpoff *et al.*, 2000). According to this theory, African, East Asian, Australian and European populations would have had relatively ancient separate ancestries. Support for this model comes primarily from fossil evidence, where continuity of certain morphological characters is claimed for the separate geographic regions between archaic and recent craniofacial morphology (Thorne and Wolpoff, 1992). Regional continuity has been suggested for the origin of Aboriginal Australian morphology, for example (Weidenreich, 1945; Coon, 1962). Under this scenario a lineage can be traced from Javanese Pleistocene specimens, such as Trinil and Sangiran, through prehistoric skulls such as the Wajak specimen from Java and the Kow Swamp skeletons from Australia, to recent Aboriginal Australians (Storm, 2001). Molecular evidence is also used to support the multiregional hypothesis. It has been suggested, for example, that the pattern of diversity found in a pseudogene on the X chromosome reflects the existence of a basal lineage in Asia, with a most common ancestor dating to around 2 million years ago (Garrigan *et al.*, 2005). This has been interpreted as demonstrating hybridisation between Eurasian archaic populations and expanding *Homo sapiens* thus providing potential support for the Multiregional hypothesis.

In contrast, the Recent African Origin or Out of Africa model suggests that all non-African populations descend from an anatomically modern *Homo sapiens* ancestor that evolved in Africa approximately 100,000 – 200,000 years ago (Stringer and Andrews, 1988). Under this model, *Homo sapiens* dispersed out of Africa and completely replaced any existing archaic populations still present outside of Africa, including Neanderthals (Stringer and Andrews, 1988; Stringer, 2002). The appearance of *Homo sapiens* is seen as a single speciation event with little or no admixture with earlier members of the genus *Homo*. The Weak Garden of Eden model represents a modified version of the Recent African Origin model, suggesting that populations may have remained small and subdivided for some time after the initial *Homo sapiens* migration out of Africa (Harpending *et al.*, 1993).

Supporting evidence for the Recent African Origin model comes both from molecular and morphological evidence. The fossil record demonstrates that the earliest *Homo sapiens* specimens are from Africa, including the Herto specimens from Ethiopia, where three partial skulls have been dated to between 154,000 - 160,000 years ago (White *et al.*, 2003). Morphological characters that have been used to support the Multiregional theory by linking archaic and recent populations in the same areas are now argued to be either retained plesiomorphies or not to be homologous (Stringer, 1992; Lahr, 1996). The majority of genetic data support the Recent African Origin model. Early studies of global mitochondrial DNA (mtDNA) diversity provided support for this model (Cann *et al.*, 1987) and more recent molecular studies have further identified a relatively recent origin of *Homo sapiens* within Africa (e.g. Ingman *et al.*, 2000; Watkins *et al.*, 2001). An analysis of the complete mtDNA sequence of 53 humans from around the world, for example, produced a neighbour-joining tree with its three deepest branches leading exclusively to sub-Saharan mtDNAs (Ingman *et al.*, 2000). An estimated date of 171,5000 ± 50,000 years BP was calculated for the date of the most common recent ancestor of mtDNA (Ingman *et al.*, 2000). In both mtDNA and Y chromosome data greater genetic variation is found among contemporary Africans than that seen in the rest of the world and the deepest splitting branches are found exclusively in African populations (Tishkoff *et al.*, 1996; Ingman *et al.*, 2000; Jorde *et al.*, 2000; Watkins *et al.*, 2001). A study of *Alu*-insertion polymorphisms determined that *Alu* gene diversity is highest in Africa but lower in Europe and Asia (Watkins *et al.*, 2001). In contrast, all non-African populations can trace their ancestry back to just three founder lineages for both mtDNA (haplogroups M, N and R) and Y chromosomes (haplogroups C, D and F) (Underhill *et al.*, 2000; Kivisild *et al.*, 2003; Oppenheimer, 2003; Forster, 2004). Beyond Africa the distribution of mtDNA and Y chromosome haplogroups is not uniform across the world. Whilst all three mtDNA founder haplogroups are present in South Asian to Australian groups, for example, only those derived from haplogroups N and R are found in West Eurasia. In the case of the Y chromosome, haplogroup F is spread widely from Europe to Australia, whilst C and D have more restricted distributions. Analysis of mtDNA taken directly from the Neanderthal type specimen gives further support for the Recent African Origin model (Krings *et al.*, 1997, 2000).

Krings *et al.* (1997; 2000) determined that Neanderthals are considerably more genetically different from all modern human populations than the latter are to one another (Krings *et al.*, 2000). This was interpreted as demonstrating that Neanderthals had contributed little or no genetic material to the modern human gene pool, thus supporting the Recent African Origin model (Krings *et al.*, 1997; 2000). A similar conclusion was reached by Harvati (2001) from a study of chimpanzee, human and Neanderthal temporal bone morphology. Harvati (2001) found that the differences between human and Neanderthal temporal bone shape were at least as great as that between the two species of chimpanzee.

Alongside the polar arguments of the Multiregional and Recent African Origin hypotheses, two intermediate theories have been postulated for the origins of *Homo sapiens*. As with the Recent African Origin model, the African Hybridisation and Replacement model predicts Africa as the place of evolution, resulting from accumulated regional genetic changes (Bräuer, 1992). Unlike the Recent African Origin model, however, Bräuer's model allows for a greater or lesser amount of hybridisation between the migrating modern humans and the indigenous archaic populations (Bräuer, 1992). Thus certain specimens from the Far East and Central Europe are identified as displaying transitional morphology between archaic and modern populations. A similar model has been proposed by Smith (1992) in which modern humans have a single place of origin, Africa. Under this Assimilation model, however, no complete replacement of the archaic populations is allowed, rather the archaic populations were assimilated with the modern humans through gene flow, admixture and changing selection pressures (Smith, 1992). The difference between the Assimilation model and that of Bräuer is that the former places greater emphasis on the overall continuity of the regional archaic populations rather than their overall replacement.

1.3.1 The Late Pleistocene dispersal from Africa

Although the various hypotheses for the evolution of *Homo sapiens* continue to be debated, most molecular and skeletal evidence points to an origin in Africa during the late Middle Pleistocene, approximately 250,000 - 130,000 years ago (Klein, 1999;

Stringer and Andrews, 1988; Tishkoff *et al.*, 1996; Ingman *et al.*, 2000; Underhill *et al.*, 2001; White *et al.*, 2003). From a single African origin, *Homo sapiens* spread across the Old World, reaching Australia by at least 45,000 years ago (O'Connell and Allen, 2004). Further debate continues, however, over the number and direction of routes taken out of Africa with both northern and southern, or both, routes championed (Klein, 1999; Lahr and Foley, 1998; Lahr, 1996; Kingdon, 1993; Stringer, 2000; Macaulay *et al.*, 2005).

Klein (1999) highlighted the dichotomy between the localised African origin of *Homo sapiens* and the widespread distribution of the species, with humans found throughout the Old World, as far as Melanesia and Australia, by approximately 60,000 – 45,000 years ago. Given a proposed date of approximately 45,000 years for the first appearance of *Homo sapiens* in Australia (O'Connell and Allen, 2004), this dispersal must have occurred relatively rapidly. Two main migration routes out of Africa are suggested, one northern and one southern (Klein, 1999; Lahr and Foley, 1998; Kingdon, 1993; Stringer, 2000). A single northern dispersal through Africa and the Levant around 45,000 years ago was favoured by Klein (1999), triggered by a technological revolution from Middle to Upper Palaeolithic technology. According to Klein, all non-African populations would be derived from this single dispersing population and the earlier presence of modern humans in the Levant during the last interglacial, as evidenced by the Skhul and Qafzeh skeletons, was only a brief and truncated geographical expansion (Klein, 1999). Kingdon (1993) also favoured a dispersal route through the Levant, but he proposed that this occurred during the Middle Palaeolithic and that humans had travelled as far as Southeast Asia by around 90,000 years ago. Having subsequently adapted to a coastal existence, humans then moved back into Africa and also southwards into Australia and Melanesia (Kingdon, 1993). Lahr and Foley (1994) alternately envisaged explicit multiple dispersal events from north eastern Africa. These separate dispersals were distinguished by their association with distinct stone tool types, the 'Mode 3' and 'Mode 4' technologies (Lahr and Foley, 1994). A first dispersal route extended northwards from Africa into south western Asia via the Nile Valley and the Sinai Peninsula. This dispersal was associated with the Upper Palaeolithic or 'Mode 4' technology found at sites such as Boker Tachtit in southern Israel and Ksar Akil in Lebanon, both dated to

around 45,000 – 50,000 BP (Mellars, 2006b). A second proposed dispersal route went east and south from Africa via the Straits of Hormuz (Bab el Mandeb) (Lahr and Foley, 1994). This route is associated with the simpler Middle Palaeolithic or 'Mode 3' technology and followed the coasts eastwards, through South Asia and into Southeast Asia and Australia. A southern dispersal route was again argued for by Stringer (2000), utilising the evidence of Middle Stone Age littoral adaptations and sea shell middens along the coast of the Red Sea (Walter *et al.*, 2000). Stringer (2000) argued that coastal expansion around the Red Sea basin could have facilitated a range of expansion of modern humans towards Australasia without necessarily using the Straits of Hormuz. A coastal pattern of dispersal has long been argued for as it would make good sense in both ecological and demographic terms (Sauer, 1962; Lahr and Foley, 1994; Stringer, 2000). Coastal environments have typically more stable ecosystems and thus would require only limited economic adaptations from one coastal location to another.

A southern dispersal out of Africa, independent of any movement of peoples across the Levantine corridor into Eurasia, is now generally considered as the most parsimonious route into Asia and beyond (Lahr and Foley, 1994, 1998; Lahr, 1996; Kingdon, 1993; Stringer, 2000; Oppenheimer, 2003). The southern route hypothesis suggests that the most likely dispersal pattern taken by early migrants from East Africa followed the coast of the Indian Ocean, across the ancient sub-continents of Sundaland and Sahul, ultimately ending in Melanesia and Australia (Stringer, 2000). The timing of the dispersal is constrained by the early dates of the colonisations of Melanesia and Australia. Humans had reached Melanesia by at least 41,000 years ago, represented by the skull found at the Niah Cave in Sarawak (Barker *et al.*, 2002). Australia was colonised by at least 45,000 years ago (O'Connell and Allen, 2004), though dates around 60,000 years ago have also been suggested (Thorne *et al.*, 1999). These early dates would require a dispersal of modern humans from Africa during the Middle Pleistocene. *Homo sapiens* have been shown to be living along the African coast of the Red Sea around 125,000 years ago, possibly exploiting marine food resources (Walter *et al.*, 2000). It is possible that they spread from there along the shorelines of Arabia and into southern Asia during, or soon after, the last interglacial (Stringer, 2000). Modern

humans may have continued following the shorelines, progressing to Indonesia at times of low sea level. By following the coastal routes the early migrants would have avoided the degree of habitat disruption faced by the inland populations during the rapid climatic fluctuations of the Late Pleistocene (Stringer, 2000). A study of allele frequency gradients attempted to place populations and individuals on the globe and found a significant association between inferred occupation sites and coastlines, suggesting that most early humans lived near large bodies of water (Amos and Manica, 2006).

1.3.2 Evidence for the southern route hypothesis

Little direct archaeological evidence has so far been found from the initial regions occupied on the proposed southern route (Mellars, 2006a). Lithic assemblages are known from the Arabian Peninsula that have affinities with technologies from the African Middle Stone Age (Petraglia, 2003). Dating of these assemblages, however, is not precise and additionally these technologies can be found associated with both *Homo heidelbergensis* and early modern humans, precluding a direct association of their presence outside of Africa with the proposed southern dispersal route (Field and Lahr, 2006). Archaeological evidence from South Asia, such as at Jwalapuram in southeast India and the microlithic assemblages from Batadomba-lena in Sri Lanka dating from around 28,000 years ago, are comparable with the so-called Howiesons Poort technology of southern and eastern Africa which dates to around 65,000 – 55,000 years ago (James and Petraglia, 2005). Although the Indian sites can only be reliably dated to around 34,000 years ago, later than the colonisation dates of Australia, current excavations at the Jwalapuram site suggest that similar industries may date from an earlier period (Mellars, 2006a). The similarities between the African Howiesons Poort technology and those found in South Asia may suggest a direct connection between the earliest human occupation of South Asia and their probable ancestors in eastern and southern Africa (Mellars, 2006a).

Stronger support for the southern route hypothesis is given by recent molecular studies that have been applied to the ideas of single or multiple dispersals (Quintana-Murci *et al.*, 1999; Endicott *et al.*, 2003a, b; Forster, 2004; Kivisild *et al.*, 2006; Forster and

Matsumura, 2005). Initially evidence from mtDNA was used to identify a single dispersal from Africa, although whether this was a northern or southern dispersal was not distinguished (Watson *et al.*, 1997). MtDNA evidence further indicated an exit route from Africa through eastern Africa and western India, with the suggestion that this was possibly the only successful early dispersal event of modern humans out of Africa (Quintana-Murci *et al.*, 1999). Around 85,000 years ago, the L2 and L3 mtDNA haplogroups expanded, leading to the successful migration from Africa (Forster and Matsumura, 2005). Haplogroup L3 subsequently gave rise to the two basal non-African clades, haplogroups M and N, which date to around 63,000 years ago (Macaulay *et al.*, 2005). The lack of other L3 lineages amongst all non-Africans suggests that the earliest human dispersal must have carried the M and N haplogroups, or that they replaced previously extant lineages (Endicott, 2003b). The time to coalescence of the major M subclusters on the Indian subcontinent centre around 47,000 years ago, and are comparable in diversity, and older than, most eastern Asian and Papuan haplogroup M clusters (Forster *et al.*, 2001). This suggests that the Indian subcontinent was settled soon after the African exodus and that there has been no complete extinction or replacement of the original settlers (Kivisild *et al.*, 2003).

Part of the rationale for the southern route hypothesis is the presence of a number of 'relic' populations that may be the descendants of the initial dispersing population out of Africa (Nei and Roychoudhury, 1993). A study by Thangaraj *et al.* (2003) looked at two of these proposed relic groups, the indigenous tribal populations of the Andaman and Nicobar Islands from the Indian Ocean. This study of a hypervariable sequence (HVS-1) of mtDNA found that the Andamanese had closer genetic affinities with other Asian populations than with Africans and that the Nicobarese were more closely related to Southeast Asians (Thangaraj *et al.*, 2003). A parallel study by Endicott *et al.*, (2003a), which analysed mtDNA from museum specimens, found further affinities between the Andaman Islanders and Asian populations. Two major mtDNA lineage groups were identified on the Andaman Islands that relate to the haplogroups M2 and M4, found commonly throughout India (Endicott *et al.*, 2003a). An extended study by Thangaraj *et al.* (2005) analysed the complete mtDNA sequence of Andaman Islanders and identified

the M31 and M32 mtDNA types which branched directly from the M haplogroup. Thangaraj *et al.* (2005) initially believed that the M31 and M32 haplogroups evolved in the Andaman Islands independently from other South and Southeast Asian populations and had been isolated since the first human penetration of the northern coastal areas of the Indian Ocean. Further screening of Indian populations by Palanichamy *et al.* (2006), however, identified the existence of two individuals of the Rajbanshi population from West Bengal that shared 3 out of 14 mtDNA coding region substitutions specific for the M31 haplogroup. This therefore suggests that the Andamanese M31 haplogroup shares a more recent common ancestor with some mainland Indian mtDNA lineages than previously thought, possibly around 50,000 years (Thangaraj *et al.*, 2006). This revised finding is still consistent with an ancient isolation of these gene pools but suggests that they may not have been part of the initial phase of the southern route dispersal. Another proposed 'relic' population of Southeast Asia, the Orang Asli of Malaysia (Bellwood, 1993) was studied by Macaulay *et al.* (2005). MtDNA types M21 and M22 were found in the Malaysian dataset that are geographically restricted branches of M that branched off from other Asian mtDNA lineages around 60,000 years ago (Macaulay *et al.*, 2005). Although caution is expressed over the dating given the time depths involved, the researchers claim that their conclusions are plausible on environmental grounds. They suggest that the region of the Malaysian Peninsula may have acted as a glacial refuge where populations could survive and maintain genetic diversity as forests would have flourished on the lowlands throughout the last glacial period (Bulbeck, 2003).

A range of genetic evidence therefore appears to support the southern route hypothesis and the coalescence dates of the M haplogroups appear to suggest a single dispersal out of Africa (Macaulay *et al.*, 2005). The various studies show that all modern Asian and European populations derive from a single subset of the L3 mitochondrial lineage in Africa, whilst subsequently diverging into the derivative M and N lineages shortly after the dispersal from Africa. The arguments centre on the fact that there is a limited amount of genetic diversity exhibited by modern Asian and European peoples compared to those in Africa (Ingman *et al.*, 2000). This dichotomy is effectively impossible to reconcile with a model of two or more distinct dispersal events.

1.3.3 The palaeoenvironment of the southern route

The exact timing of the southern dispersal around the Indian Ocean rim is not known, but it is believed to have taken place during Oxygen Isotope Stage 4 (OIS 4), approximately 71,000 – 59,000 years ago (Field and Lahr, 2006). During this time the sea levels were lowered to 80-88 m below modern day levels (Siddall *et al.*, 2003), exposing the Sunda Shelf and large parts of western South Asia. Although sea levels were lowered the Red Sea was never disconnected from the Arabian Sea at the point of the Bab al Mandab Straits. Glaciation would probably have resulted in a suppression of the monsoon system that usually provides seasonal moisture across the Indian Ocean basin, resulting in greater aridity along much of the Indian Ocean rim (Field and Lahr, 2006). Along with the general trends, however, there was also regional variation in both temperature and humidity during and after glacial episodes, resulting in periods of wetness in the desert environments of South Asia (Overpeck *et al.*, 1996). Rapid transitions between arid and wet episodes would have had an impact on the subsistence regimes and mobility of populations residing in these regions at this time (Field and Lahr, 2006).

1.4 Human dispersals

Having likely evolved in Africa, *Homo sapiens* are now found all across the Earth. How they reached the different continents and when, continues to be a source of much debate. From arguments concerning whether it was a single or multiple migrations that left Africa, to whether a single or multiple immigrants colonised Australia, many models have been constructed for the origins of particular regions. The main models for each region discussed in this study are given below, along with some of the evidence used to define them. The evidence for the timings and methods of colonisation come from a combination of archaeology, linguistics, genetics and where possible the skeletal remains of these early migrants.

1.4.1 South Asia

The Indian subcontinent would have acted as a major corridor for dispersing migrants out of Africa along the proposed southern route (Majumder, 2001). Dating of the first occupation of India is unclear, but coalescence dates for Indian specific branches of mtDNA haplogroup M provide a possible entry date of at least 60,000 years ago (Chaubey *et al.*, 2007). Archaeological evidence also indicates an early settlement of India during the Late Pleistocene, with evidence of two lithic technologies known as Middle Palaeolithic and Upper Palaeolithic (James and Petraglia, 2005). In Nepal, for example, the site of Arjun 3 has produced a Levallois-based industry containing scrapers, points and blades that is older than around 30,000 years ago (Corvinus, 2002). By around 50,000 years ago occupation appears to have spread to many parts of the subcontinent (Misra, 2001). Some of the earliest human fossils from South Asia, dating to around 31,000 years ago, have been found at the site of the Fa Hien Cave in Sri Lanka (Deraniyagala, 1992). India today contains a wealth of genetic, cultural and linguistic diversity. The population of India is split into tribal groups, that constitute approximately 8% of the total population, and non tribal groups (1991 Census of India). The tribal groups are widely considered to be the original inhabitants of the subcontinent and can be split into three linguistic families, the Austro-Asiatic, Dravidian and Tibeto-Burman (Majumder, 2001). The non tribal populations of India predominantly speak languages that belong to the Indo-Aryan and again Dravidian families (Majumder, 2001).

India has undergone many influxes of people either as immigrants or invaders (Kivisild *et al.*, 2003). Following the Late Pleistocene dispersal, a second migratory event has been proposed around 10,000 years ago with proto-Dravidian speaking Neolithic farmers migrating into South Asia (Watkins *et al.*, 1999). A third migration of Indo-European speaking 'Caucasoids' from West-Central Asia, entered around 3,500 years ago (Watkins *et al.*, 1999). The genetic diversity in India is only second to Africa (Majumder, 1998), though it remains unclear whether the variation seen between different Indian populations primarily reflects their long term differentiation or is due to relatively recent migrations from outside of the region (Kivisild *et al.*, 2003). The basic clustering of Indian mtDNA lineages has been determined by some researchers as not reflecting specific language or caste groups (Bamshad *et al.*, 2001). An analysis of mtDNA, the Y chromosome and one autosomal locus has revealed that both caste and tribal groups derive largely from the same genetic heritage of Pleistocene southern and western Asians and have received limited gene flow from external regions since the Holocene (Kivisild *et al.*, 2003). A later study, however, suggested that the patterns of genomic diversity found within the tribal populations inhabiting differing geographic locations reflects heterogeneous origins of differing linguistic groups (Cordaux *et al.*, 2004).

1.4.2 Southeast Asia

Southeast Asia broadly consists of Myanmar (Burma), Thailand, Cambodia, Laos, Vietnam, Malaysia and the islands of Indonesia. The population history of the region is complex because of the various migration processes and the possible intermixing of populations since prehistoric times (Matsumura, 2006). The dating of the first occupation of Southeast Asia is unclear, however it can be assumed that it was occupied prior to the dates for Australia and Melanesia as it is obvious that any dispersal into Australia had to go through Southeast Asia (Hanihara, 2006). Possibly the earliest direct evidence for humans in Southeast Asia is the Niah Cave skull from Sarawak, radiocarbon dated to approximately 40,000 years BP (Kennedy, 1977). The skeletons found at Moh Khiew Cave in Thailand have been dated to c25,800 ± 600 BP

(Matsumura and Pookajorn, 2005) and the remains from Tabon Cave on Palawan Island, the Philippines, date to around 16,500 BP. Many studies of pre-neolithic human remains from Southeast Asia consider the indigenous inhabitants of the region to be typical of 'Australo-Melanesians'. The Niah Cave specimen, for example, is said to be most similar to Tasmanian morphology (Brothwell, 1960), and the Tabon remains have been compared to 'Australo-Melanesians' (Macintosh, 1978). Matsumura (2006) has analysed skeletal evidence from Southeast Asia, including the Moh Khiew Cave remains and suggests that there is morphological evidence of a link between the indigenous people of Southeast Asia and the 'Australo-Melanesian' lineages. He further suggests that that these specimens, along with the Tabon and Niah fossils, can be regarded as an early group of Southeast Asians who originated in late Pleistocene Sundaland and were the ancestors of the modern Melanesian and Australian aboriginal peoples (Matsumura, 2006). This assessment is not however concurrent with all researchers. Storm (1995), for example, examined the Wajak skulls from Gunung Lawa, Java, dating from approximately 6,500 BP, and concluded that they showed more similarity to modern Indonesians than to Australians.

Present day Southeast Asians are biologically heterogeneous (Lahr, 1996), possibly reflecting a complex history of migration in the region. No clear consensus exists, however, regarding the origins of the present day inhabitants of Southeast Asia. The main arguments concern the affinities of the indigenous peoples of Southeast Asia and how the modern phenotype evolved. The classic view is that Southeast Asia was originally occupied by people phenotypically similar to 'Australo-Melanesians', who were then replaced by an immigrant group of people from somewhere in southern China (Bellwood, 1997). This is known as the Immigration or Two-Layer model and is supported by genetic, linguistic and archaeological evidence. Classic markers and mtDNA analyses, for example, have demonstrated similarities between Chinese and Southeast Asian samples (Cavalli-Sforza *et al.*, 1994; Tan, 2001). Archaeological and linguistic studies have linked the expansion of the Austronesian and Austroasiatic language families with the dispersal of rice-cultivating populations from Southern China or Taiwan during the Neolithic period (Renfrew, 1992; Bellwood, 1997; Blust, 1996).

Alternate hypotheses for the origins of the present day Southeast Asians are based upon dental and cranial morphology and are known as the Regional Continuity or Local Evolution models (Turner, 1992: Hanihara, 1993, 1994). These models argue that the present day inhabitants of Southeast Asia evolved from earlier groups living within the region. Turner (1992) assessed the non-metric dental traits of early and modern Southeast Asians and determined that they both shared the so-called 'sundadont' dental complex. According to Turner, this is the ancestral dental complex to the 'sinodont' complex found in Northeast Asia. Using craniometric techniques, Hanihara (1993, 1994) argued that what he called 'Proto-Malayans' were the original source population for modern Southeast Asians and found no presence of an 'Australo-Melanesian' lineage in their ancestry. Both Turner and Hanihara suggested that modern Southeast Asians had therefore evolved in situ with local adaptations, rather than having been extensively admixed with immigrants from Northeast Asia.

1.4.3 Australia

For much of the Pleistocene Australia, New Guinea and Tasmania were connected as a single continent known as Sahul. At this time thousands of kilometres of additional coastline were available for humans colonising Sahul, along the northwestern and northern coastlines of the continent (Curnoe, 2006). Travel distances from Southeast Asia would also have been shorter, for example a direct route from Timor may only have been around 100km (Curnoe, 2006). Two possible routes have been suggested for the colonisation of Sahul (Birdsell, 1977). The first took a northerly route from modern Sulawesi to northern Sahul (New Guinea), and south into Australia. The second possible route, taken instead of or in addition to the first, followed a more southerly path through modern Java via Timor to the northwest coast of Australia. The colonisation of Sahul is thought to have taken place some time between 60,000 - 45,000 years ago (Bowler *et al.*, 2003; O'Connell and Allen, 2004). Only dates between 42,000 - 45,000 years are well supported by the archaeological record and the older dates continue to be debated (O'Connell and Allen, 2004). Tasmania was one of the last regions of Sahul to be colonized, with the earliest evidence of occupation dating to around 35,000 BP at

Warreen Cave (Porch and Allen, 1995). This comparatively late occupation is due to the sea level in the Bass Strait, separating Tasmania from mainland Australia (Lambeck and Chappell, 2001). Tasmania was completely isolated from Australia until approximately 32,000 BP and then again from 14,000 years ago (Lambeck and Chappell, 2001).

Controversy and debate surrounds the dating and the biological affiliation of the first Australians (Curnoe and Thorne, 2006; Brown, 2000). The earliest date claimed for human remains is between 57,000 – 71,000 years ago for the Lake Mungo 3 (LM3) skeleton (Thorne *et al.*, 1999), however more conservative dates of between 40,000 – 50,000 years, or possibly even younger, are also considered (Bowler *et al.*, 2003). The morphological diversity found within the early Australian specimens is similarly disputed. Fossil Australian crania have been interpreted as demonstrating considerable morphological variation with the specimens being classified into two main groups, one 'gracile' and the other 'robust'. The gracile group is represented by the LM3 individual, along with the Lake Mungo 1 and the Keilor individuals (Thorne and Curnoe, 2000). The 'robust' group, including the Kow Swamp specimens, are younger than the Lake Mungo specimens, with the Kow Swamp individuals dated to between around 22,000 – 9,000 years ago (Stone and Cupper, 2003; Thorne and Macumber, 1972). Thorne is a strong advocate of the two population approach and interprets the LM3 skeleton as being a gracile male and representing a population who initially occupied Australia during the Pleistocene (Thorne, 1976; Thorne and Curnoe, 2000). An alternative opinion is given by Brown (2000) who argues against two distinct populations, suggesting rather that there is nothing in the original description of LM3 to indicate that it has a gracile morphology or that it contrasts distinctly with the Kow Swamp specimens.

The debate regarding morphological variation in the earliest Australians has led to a number of proposed models for the first settlement of the continent (Bowdler, 1993; Flannery, 1994; O'Connell and Allen, 1998; Pardoe, 2006). Early models emphasise multiple waves of migration into Australia to explain the differences in morphology

(Birdsell, 1967; Tindale, 1974). A tri-hybrid model is suggested, for example, where three distinct waves of migrants entered Australia and the observed morphological variation is derived from these differing founding populations (Birdsell, 1967, 1993; Tindale, 1974). Birdsell (1993) identified three main groups of Australians, which he termed 'Negrito', 'Murrayians' and 'Carpentarians'. He proposed that they entered Australia at different times and in that order. Birdsell (1993) proposed that the Negritos were the ancestors of New Guinean populations and are represented by the gracile Lake Mungo skeletons. The Murrayians were thought to inhabit the southeastern part of the continent around the Murray River and are represented by the Kow Swamp skeletons. The third group, the Carpentarians, were said to have moved over the northern part of Australia more recently, occupying most of the northern half of the continent (Birdsell, 1993). A similar di-hybrid model was suggested by Thorne (1976), again based upon the morphological contrasts he observed in the fossil remains. Under this model the skeletal evidence is interpreted as showing a period of initial occupation of the continent by a gracile group who are later joined on the continent by more robust migrants (Thorne and Curnoe, 2000). Archaeological evidence is used to support the sequential migration proposals, with the appearance of a new tool type, the edge-ground axe, appearing in the fossil record between 20,000 – 30,000 years ago (Mulvaney and Kaminga, 1999). This technology is claimed to have been imported to Australia from Asia, brought by the migrants into Australia (Thorne and Curnoe, 2000). The observed variability in contemporary Australians is thus formed by the mixing of the new migrants with the earlier, more gracile Australians.

Some tentative support for the tri-hybrid model is given by certain molecular studies (Redd and Stoneking, 1999). In their study of two hypervariable segments of mtDNA, Redd and Stoneking (1999) suggested that Australian and southern Indian populations derive from the same ancestral population, whereas the highland New Guinea population derives from a completely different ancestral group (Redd and Stoneking, 1999). The separation between the Australian and Indian populations was a more recent event than that between the Australian and New Guinean populations. They interpret the Australian affinity with southern India as reflecting a migration from an Indian

source that reached Australia but not New Guinea (Redd and Stoneking, 1999). A recent study of mtDNA also raises the possibility of a three population based model, but does not directly test Birdsell's model (van Holst Pellekaan and Harding, 2006). Five major maternal haplogroups are identified in this study which could reflect different migratory events, but the authors state that there is the additional possibility of a founding group that contained diverse mtDNA lineages (van Holst Pellekaan and Harding, 2006). MtDNA taken directly from the LM3 and Kow Swamp skeletons has additionally been used to support a multiple founding population model (Adcock *et al.*, 2001). It was found that the mtDNA of these specimens lay outside of the range of sampled living humans, and represents mtDNA forms that may predate the fixation of the lineage found in all living people. All other Australian fossils tested were within the range of modern Australians. This could be interpreted as being consistent with the di-hybrid or tri-hybrid models. The study has been criticised, however, in particular due to the lack of confirmation of results by alternate laboratories (Cooper *et al.*, 2001).

One of the problems with the multiple migration scenarios is that the skeletal remains from the terminal Pleistocene/early Holocene show greater levels of morphological variation than those from the later Holocene, requiring a loss of diversity over time. An alternate model claims a single founding group for the Aboriginal people (Pardoe, 2006) in which the morphological variation found in the skeletal record is seen to be derived from change and adaptation within Australia following this single founding event. A specific unitary model whereby diversification occurs due to evolutionary processes is proposed by Pardoe (2006). In particular, reproductive isolation resulting from specific marital patterns is given as a causal factor for the perceived differences in the Australian fossils. Diversification is heightened by population size, ecological conditions and differential access to high protein animal resources (Pardoe, 2006). The diversity seen in the morphology of present day Australians is echoed in the high diversity found in the mitochondrial genome (Ingman and Gyllensten, 2003). This has been interpreted as possibly reflecting subdivision from a single group into many as a result of isolation, before or shortly after arrival on Sahul (Ingman and Gyllensten, 2003). The genetic data can therefore also be seen to support a single founding population which subsequently

diverged due to isolation and drift. Similar lines of evidence have been interpreted in various ways and the genetic evidence does not give definitive support for either the single or multiple founding population models for the colonisation of Australia.

Molecular studies have additionally sought to discern whether New Guinea and Australia were settled by the same founding population. Genetic isolation of Australians has been suggested by studies of various regions of mtDNA (van Holst Pellekaan *et al.*, 1998; Huoponen *et al.*, 2001; Main *et al.*, 2001). Separate studies have shown Australians to be genetically more similar to New Guinean populations than to African and Asian populations (van Holst Pellekaan *et al.*, 1998; Ingman and Gyllensten, 2003). A remote common ancestry between contemporary Melanesians and Aboriginal Australians was supported by a study of human leukocyte antigens (HLA) (Main *et al.*, 2001). Huoponen *et al.* (2001) found sub-branches of larger clusters of mtDNAs that included other Australians and/or New Guinean haplotypes and concluded that Australian and New Guinean populations may once have shared an ancient ancestral population, but they had rapidly diverged from each other once separated. As stated above, the study by Redd and Stoneking (1999) did not support a close relationship between Aboriginal Australians and the people of New Guinea, rather they found greater similarity between Australians and groups from south India. In contrast to this, an alternate study comparing mtDNA sequences from Australia, New Guinea and South Asia found no evidence of substantial gene flow from the Indian subcontinent (van Holst Pellekaan *et al.*, 2006). Again the molecular evidence is unclear on the nature of the founding population of Sahul, but the evidence appears to favour a single ancestral population for both Australia and New Guinea that diversified very soon following the colonisation of the continent.

1.4.4 Oceania 40,000 BP – 3,500 BP

The region of Oceania can be split into two areas, Near and Remote Oceania, both in terms of geography and its demographic history (Green, 1991). Near Oceania includes New Guinea, New Britain, New Ireland, the Bismarck Archipelago and the northern Solomon Islands (Green, 1991). Remote Oceania covers the remaining territory,

including the more southern and eastern islands of Melanesia such as New Caledonia, Vanuatu, Micronesia and Polynesia. Both Austronesian and Papuan (non-Austronesian) languages are spoken in Near Oceania whilst only Austronesian languages are spoken in Remote Oceania (Kirch, 2000). As with Australia, Near Oceania was initially colonised as part of the south-eastern expansion from Africa during the Late Pleistocene. A date of approximately 40,000 BP is given for a site situated on the Huon Peninsula of northern New Guinea (Groube *et al.*, 1986), and a similarly early settlement date of 39,500 BP is found at the site of Buang Merabak on New Ireland (Leavesley *et al.*, 2002). Settlement had reached as far as the northern Solomon Islands by approximately 29,000 BP (Hurles *et al.*, 2003). Remote Oceania was not settled until much later, at around 3,500 BP.

Although Australia and New Guinea were connected during periods of low sea levels, initial colonisation of the islands of Melanesia would still have required sizeable sea voyages to reach some of these islands from Southeast Asia. The earliest populations of northern Island Melanesia were small groups of hunter gatherers who settled the interiors of the large islands intermittently (Pavlides and Gosden, 1994). Archaeological evidence, mainly from small, intermittently occupied, rock shelters suggests that there was a low population density (Gosden, 1993). No large permanent villages are found until the advent of the Lapita cultural complex around 3,500 BP and the settlement pattern suggests a strong inland orientation, though coastal resources were regularly exploited (Kirch, 2000). The cultivation of tree crops and other plants was also underway by about 9,000 BP, making the region an important early centre for plant domestication (Kirch, 2000). No pottery is found in Island Melanesia at this time (Kirch, 2000). Some level of continuing contacts between the diverse islands is indicated by the movement of obsidian over considerable distances after approximately 20,000 BP (Gosden, 1993). Obsidian flakes sourced in New Britain are found in New Ireland indicating some form of trade or exchange networks.

Although contact occurred, the indigenous peoples of Melanesia were nonetheless extremely diversified after 30,000 or more years of settlement in the region. Evidence

for such diversification comes from the complex linguistic record of Near Oceania, with at least twelve distinct language families in existence and hundreds of mutually unintelligible languages (Kirch, 2000). These languages are grouped together as Non-Austronesian or Papuan languages and are today concentrated in the interior of New Guinea, with some remaining in the Bismarck Archipelago and Solomon islands (Kirch, 2000). Foley (1986) suggests that this great linguistic diversity comes from the long time depth of human occupation in Near Oceania, combined with geographic factors favouring isolation. Along with languages, the people of Near Oceania are also biologically diversified. Near Oceanic populations have the greatest genetic diversity, for example, of the whole of the Melanesia region (Robledo *et al.*, 2003). The overall implication of the demographic history of Near Oceania during this time is that the small island populations were generally isolated with only some contact between population groups.

An apparent paradox exists in the settlement patterns of Near Oceania for the first 40,000 years (Kirch, 2000). Except for the Highlands of New Guinea, high population levels were never reached in Near Oceania although the region was occupied for a long time period on large and resource rich islands. Even with the relatively low population rates known for hunting and gathering populations it is suggested that a sizeable population could easily have arisen in Near Oceania (Kirch, 2000). The archaeological record, however, provides no evidence of numerous or densely settled populations. This contrasts strikingly with the demographic situation in the Remote Oceania islands once they are occupied after around 3,500 BP when permanent villages appear (Kirch, 2000). The explanation provided by Kirch (2000) is the pernicious effects of malaria and other infectious diseases. Several species of malaria parasite (*Plasmodium*) and their mosquito vectors are confined to Near Oceania, at least two of which (*P. vivax* and *P. malariae*) probably accompanied the first human settlers of Sahul. Evidence of this comes from the genetic mutations found in the blood systems of Near Oceanic populations that have been selected for because they confer partial resistance to the disease (Martinson, 1996). Population levels may have been regulated by endemic malaria, primarily through the continual mortality of individuals before they could reach

reproductive age (Groube, 1993). Another important event that may have influenced the demographic history of the Near Oceanic populations was the violent eruption of Mount Witori in New Britain around 3,600 years ago (Spriggs, 1997). This volcanic eruption was one of the most explosive to occur during the time that modern humans have evolved and devastated parts of the Bismarck Archipelago and New Britain. Cultural discontinuity followed the eruption, particularly on New Britain, with changes in lithic technology, land use and settlement patterns (Kirch, 2000). One important change is that no ceramics are found in archaeological levels prior to the eruption, whereas soon after the event a style of highly decorated pottery called Lapita appears suddenly (Torrence *et al.*, 2000).

1.4.5 Oceania 3,500 BP – 1,200 BP

As mentioned in the previous section, sometime around 3,500 BP a new culture, known as the Lapita cultural complex, appears in the archaeological record of Oceania. The Lapita culture is defined by a decorated pottery and is named after an excavation site in New Caledonia (Kirch, 2000). Previously unoccupied coastal niches were now settled and the cultural complex introduced new features such as permanent villages, fishhooks, sea going canoes and a range of horticultural crops and domesticated animals including dogs, chickens and rats (Hurles *et al.*, 2003). Debate continues regarding the origins of the Lapita cultural complex and is argued by some to have originated within Island Melanesia, in particular the Bismarck Archipelago, between 3,000 – 3,500 BP (Terrell *et al.*, 2001). Other archaeologists argue for an origin approximately 6,000 years ago in Southern China with the Lapita culture spreading into the Pacific associated with agriculture and Austronesian languages (Diamond and Bellwood, 2003).

The settlement of Polynesia was one of the most recent major migration events by humans, occurring within the last 3,000 years. The islands of Polynesia range from Hawaii in the north to Easter Island in the South, Fiji in the west and New Zealand in the south. The earliest Lapita sites are found within Near Oceania, however within 200 years sites appear in parts of previously uninhabited Remote Oceania including Vanuatu, New Caledonia and Fiji (Hurles *et al.*, 2003). From the archaeological evidence it is

possible that there was a pause in settlement of 500 to 1,000 years before permanent occupation of the eastern most islands of Polynesia occurred (Kirch, 2000). The first islands of Eastern Polynesia to be settled included the Cook and Society Islands and the Marquesas Group (Kirch, 2000). The more peripheral islands of Hawaii, Easter Island (Rapanui), and New Zealand (Aotearoa) were the last to be settled. By the time of these later settlements the Lapita pottery was no longer being made (Kirch, 2000). In contrast to Near Oceania, population densities were high in much of Polynesia, possibly due to the lower incidence of pathogens (Kirch, 2000).

A number of models exist for the origins of the Polynesians and the settlement of Remote Oceania, though most are not mutually exclusive (Hurles *et al.*, 2003). The 'Express Train' model proposes that the Polynesians ultimately derive from populations in southern China where the development of a farming economy during the early Holocene stimulated a demographic expansion (Bellwood, 1978; Diamond, 1988). These proto-Polynesians reached Taiwan by about 6,000 years ago and then spread to the Philippines, eastern Indonesia and New Guinea by about 3,500 years ago. Following dispersal to Near Oceania, the first occupation of Remote Oceania began with Vanuatu and Fiji, colonised by around 3,200 BP. This model is linked to the spread of the Austronesian languages which evolved in South China or Taiwan (Blust, 1995; Gray and Jordan, 2000). The movement from East Asia was rapid with few pauses along the route. Only limited genetic mixing would have occurred between the incoming Austronesians and the indigenous people of Southeast Asia and Melanesia (Cox, 2005). A second model is that of the 'Slow Boat' which suggests that the proto-Polynesians originated in island Southeast Asia during the Late Pleistocene (Oppenheimer, 1999). Sea level rises during the last glacial period flooded large parts of the Sunda shelf and resulted in a movement of the Austronesian speaking people out of coastal Southeast Asia into northern Melanesia. This model predicts considerable genetic admixture between the Austronesians and the indigenous inhabitants of Melanesia (Oppenheimer, 1999). An island Southeast Asian source for the present day Polynesians, however, does not have support from linguistics or archaeology and is largely argued for on genetic grounds (Oppenheimer, 1999). Cox (2005) examined mtDNA from extant Indonesians

and concluded that the data suggests a preferred origin of the proto-Polynesians in southern China and Taiwan rather than eastern Indonesia. The evidence from mtDNA therefore seems to favour the 'Express Train' model for the colonisation of Remote Oceania (Cann and Lum, 2004).

1.4.6 'Australo-Melanesians' and Southeast Asian Negritos

The term 'Australo-Melanesian' is commonly used in craniometric studies to refer to either the recent indigenous people of Australia, New Guinea and island Melanesia, or the people of that regional phenotype. In a study of 53 human groups from Southeast Asia and Oceania, for example, Pietrusewsky (1994) found that Australians and New Guineans clustered together in what he termed an 'Australo-Melanesian' group. The term is also sometimes used in relation to the indigenous people who were thought to be the original inhabitants of Southeast Asia (Matsumura, 2006). The identification of skeletal remains as 'Australo-Melanesian' or 'Australoid' creates the question of whether such distinct populations ever existed as discrete entities (Tayles and Oxenham, 2006). Collections of crania from around the Southeast Asian and Oceanic regions have been ascribed to such various vague classifications, without consensus of what characteristics belong to each of them. A collection from Lang Cuom, North Vietnam, for example, have been described as being 'modified Australoid', 'more or less Mongoloid' and 'mixed Negrito' (Coon, 1962). Even though the term 'Australo-Melanesian' does not have a distinct definition and is described by Bellwood (1997) as an idealised model, it continues to be used as a legitimate term by many researchers.

The present day populations of Southeast Asia known as 'Negritos' are often cited as 'relic' populations of these 'Australo-Melanesians' (Bellwood, 1997), and are therefore interesting in the study of the Late Pleistocene migration. Southeast Asian Negritos have long been presumed to represent the surviving remnants of what was once a more widespread and homogenous population (Turner and Eder, 2006). 'Negritos' are characterised by a hunting and gathering lifestyle and the shared physical characteristics of a short stature, dark skin and curly hair. They are found today across Southeast Asia from the Andaman and Nicobar Islands, to the Malay Peninsula and the Philippines.

Within the Philippines, for example, there are approximately two dozen groups including the Mamanwa of Mindanao and the Agta or Aeta, found in northern, eastern and west central Luzon (Turner and Eder, 2006). The Negrito groups are considered by some to be the descendents of the first migrants out of Africa during the Late Pleistocene (Nei and Roychoudhury, 1993). Other researchers have argued that the shared characteristics of the Southeast Asian Negritos are the result of long term, local evolutionary development under similar ecological conditions (Rambo, 1984).

Several groups from South and Southeast Asia have been postulated as members of the 'relic' populations. The Orang Asli, especially the Semang, are the aboriginal inhabitants of the Malay Peninsula and the principal 'relic' group found in Southeast Asia (Bellwood, 1993, 1997). The Semang are considered 'Negrito' foragers, with a characteristic short stature, dark skin and woolly hair phenotype (Rayner and Bulbeck, 2001). Bulbeck (1999) suggested that the Semang could be viewed as being among the dwarfed survivors of an ancient tropical population which had once spread around the Indian Ocean. This view is supported by similarities in dental morphology found between the Semang and the Philippine 'Negritos', as well as South Asians in general (Rayner and Bulbeck, 2001). The dental morphology displayed by the Semang is considered to be conservative in evolutionary terms, and therefore probably once widely distributed throughout Southeast Asia (Rayner and Bulbeck, 2001). Results of mtDNA analyses indicate that the Orang Asli harbour 'relic' mtDNA lineages, with time depths of about 40,000 to 63,000 years (Macaulay *et al.*, 2005). The restricted distribution of these mtDNA lineages makes it very likely that they diverged around that time within mainland Southeast Asia.

The Veddah of South Asia are considered by some to be the indigenous, hunter-gatherer inhabitants of Sri Lanka (Bulbeck *et al.*, 2003). They are thought to be biologically distinct from the Singhalese and Tamil speaking groups of Sri Lanka, and to be the descendents of the first inhabitants of the island (Deraniyagala, 1992). The Veddah are said to have morphological affinities with Southeast Asian Negritos and Australian Aborigines (Howells, 1959, 1993), suggesting that the indigenous populations of

Southeast Asia once occupied the southern Indian subcontinent (Lahr, 1996). Admixture between the Veddah and the Singhalese, however, is evident from the fact that the Veddah today speak Singhalese rather than a specific Veddah language, and that today the majority of Veddah practice a mixed farming economy rather than a hunter-gatherer lifestyle (Bulbeck, 2003). The arrival of the Singhalese language to Sri Lanka dates to over 2000 years ago, suggesting a considerable time period of interaction between the Veddah and the more recent inhabitants of Sri Lanka (Kennedy, 2003).

A further example of a possible 'relic' population in South Asia is the Kusunda tribe of central Nepal. They are described as being short in stature and having a darker skin colour than surrounding South Asian tribes (Whitehouse *et al.*, 2004). Although now spoken by only a few remaining individuals, the Kusunda language is recognised as being a member of the Indo-Pacific language family, and is today a geographic isolate in South Asia (Whitehouse *et al.*, 2004; Greenberg, 1971). Indo-Pacific languages are currently found in great numbers on New Guinea and other Pacific islands including New Britain, New Ireland and the Solomon Islands. They were also the language of Tasmania until 1876 (Whitehouse *et al.*, 2004). Due to its isolated position in South Asia, it would seem plausible that the language of the Kusunda is a linguistic remnant of the dispersal from Africa, through South Asia and finally to New Guinea and Australia.

The Kusunda language is thought to share grammatical and lexical affinities with surviving languages found in the North Moluccas, the lesser Sunda islands and the Andaman Islands (Ruhlen, 1991; Whitehouse *et al.*, 2004). The inhabitants of the last group, the Andaman Islands, are amongst the best candidates for being the descendents of the pre-Neolithic Southeast Asians, with their geographic isolation aiding their survival (Thangaraj *et al.*, 2003). The Andaman Islands are situated in the Indian Ocean, in an arc between Burma and Indonesia. Along with a shared linguistic history, the Andaman Islanders share the similar distinctive phenotype of the Kusunda. They are short in stature, with a dark pigmentation and unusual hair morphology. Differing interpretations for the affinities of the Andaman Islanders have been given. Victorian anthropologists, such as Dobson (1875), suggested a recent African origin due to the

perceived phenotypic similarities to African pygmies (Endicott *et al.*, 2003a). Recent genetic data, however, has shown that the Andaman Islanders have closer affinities with Asian rather than African populations, with ancient mitochondrial DNA lineages that have likely been isolated since the initial penetration of the northern coastal areas of the Indian Ocean approximately 50,000 to 70,000 years ago (Endicott *et al.*, 2003a, b; Thangaraj *et al.*, 2003, 2005).

Within the same archipelago as the Andaman Islands and positioned just over 100km south of them, lie the Nicobar Islands. The inhabitants of these islands, the Nicobarese and the Shompen, have also been hypothesised to be direct descendents of early human dispersals into Southeast Asia (Cavalli-Sforza *et al.*, 1994). The identity of the ancestors of the Nicobarese remains controversial, however, and phenotypically they do not resemble their close neighbours the Andaman Islanders (Prasad *et al.*, 2001). Linguistically, the dialects of the Nicobarese language belong to the Austro-Asiatic language family (Das, 1977). More specifically they have been linked to the Mon-Khmer languages of Cambodia and Vietnam (Justin, 1994; Bellwood, 1997). A recent genetic study indicated that their mtDNA haplotypes are most closely related to those of Cambodians, with whom they share a unique mtDNA haplotype (Prasad *et al.*, 2001). A later study by Thangaraj *et al.* (2005) found that most Nicobarese mtDNA lineages belonged to either of the two common haplogroups B and F, which are specific to East Asia. In contrast to the long isolation of the Andamanese, the Nicobarese show a close genetic relation with populations in Southeast Asia, suggesting a more recent arrival from the east during the past 18,000 years (Thangaraj *et al.*, 2005).

1.5 The biological effects of human dispersal

Human dispersal has been studied from many different perspectives, both social and biological. The earliest studies of the biological impact of dispersal date back to the early 20th century with studies on cranial plasticity in immigrants to the United States by Fishberg (1905-07) and Boas (1912). Cranial plasticity refers to the idea that the cranium responds to environmental forces during growth and development, and thus can be shaped primarily by epigenetic effects (Sparks and Jantz, 2002). Although Boas'

study of Eastern and Southern European migrants to New York City is better known, it was preceded by smaller scale study of immigrant Jews by Fishberg (1905-07). Fishberg observed that the specific environment had an effect on the human phenotype, with first generation migrants to the United States being taller than natives from Eastern Europe, and second generation migrants being taller still. Boas (1912) conducted similar research, measuring head dimensions and stature of children and adults by age of immigration. Boas' findings agreed with Fishberg's on the change in stature related to immigration but additionally found changes in the cephalic index among first and second generation migrants to the United States. This latter finding contrasted with that of Fishberg (1905-07) who argued that the shape of the head depended only on race and heredity whilst Boas argued against the fixity of racial characteristics for the skull. Boas' (1912) work has recently been reanalysed by two independent studies, Sparks and Jantz (2002) and Gravlee *et al.* (2003), both of which also came to divergent conclusions. The findings of Gravlee *et al.* (2003) supported those of Boas, with three of four ethnic groups studied showing a small but significant difference in cephalic index between foreign born and US born children. Sparks and Jantz (2002), however, claimed a discrepancy with Boas' findings and stated that his results could no longer be used to support arguments of plasticity in cranial morphology. In a review of this literature, Relethford (2004a) criticised the methods of the Sparks and Jantz study and argued that there is statistical support for Boas' claim of cranial plasticity. It appears that cranial plasticity is a feature of human migration but it is only of relatively small magnitude and not sufficient to erase the underlying pattern of population relationships.

1.5.1 Genetic diversity and geographic dispersal

Much of the evidence to support a recent African origin of modern humans comes from patterns of genetic variation found across the globe (Liu *et al.*, 2006). These patterns of human diversity are intrinsically linked with the process of geographical expansion and dispersal. Isolation by distance and divergence from a shared population history are two sources of population substructure. The isolation by distance model predicts that human subpopulations will reflect geographic separation in the pattern of their between group biological distances (Wright, 1943). Isolation will eventually result in a greater genetic

similarity between geographically proximal populations and increasing genetic differences between groups that are further and further apart (Crawford, 1998). Population history will be erased by isolation by distance as populations approach migration-drift equilibrium. Various studies on genetic polymorphisms have demonstrated a strong association between genetic distance and geographic distance between modern human populations (Eller, 1999; Relethford, 2001; Ramachandran *et al.*, 2005). Eller (1999) found that geographic distance accounted for almost 60% of world wide inter-population genetic relationships, using short tandem repeat data. Within continents the results were less robust (Eller, 1999), suggesting that populations have not reached migration-drift equilibrium. Excess heterozygosity was also found within Africa, a pattern previously noted by Stoneking *et al.* (1998).

The observed positive relationship between geographic and genetic distances has usually been attributed to the theoretical model of isolation by distance which is valid only at equilibrium between migration, mutation and drift. The relatively short evolutionary history of modern humans suggests that there has not been enough time to reach equilibrium between the extremes of human geographic range, as demonstrated by Eller (1999). An expansion of modern humans from a single centre is an alternative way of producing a global correlation between geographic and genetic distances. Ramachandran *et al.* (2005) extended beyond the correlation of geographic distance and genetic differentiation to further explain the explicit patterns found. Fitting a linear regression of F_{ST} (the measure of genetic distance used) on geographic distance produced a R^2 value of 0.5882, however incorporating a likely path of dispersal from Africa increased this value to 0.7834 (Ramachandran *et al.*, 2005). No geographic origin outside of Africa accounted as well for the observed patterns of genetic diversity (Ramachandran *et al.*, 2005). Such geographical expansion may have happened in many small steps, with each such migration involving a sampling from the previous subset of the original populations. This sampling would have led to a stepwise increase in genetic drift and a concomitant decrease in genetic diversity and a pattern of serial founder effect (Harpending and Rogers, 2000; Ramachandran *et al.*, 2005).

Ramachandran *et al.*, (2005) found by simulation that the geographic pattern of heterozygosities was consistent with a serial founder effect starting at a single origin.

Geographic distance, as well as genetic distance, can predict the patterns of molecular diversity found in modern human populations (Prugnolle *et al.*, 2005). Taking Ethiopia as a starting point, due to the discovery there of the earliest human fossil remains, Prugnolle and colleagues (2005) computed geographic distances within the context of modern human settlement. An extremely strong negative correlation was found between geographic distance from East Africa and genetic diversity, with populations geographically furthest away from Ethiopia characterised by the lowest genetic variability (Prugnolle *et al.*, 2005). The highly significant relationship explained 85% of the observed genetic variance on a world wide scale and was interpreted as being only compatible with a colonisation of the world by a single population from Africa. The constant loss of genetic diversity along colonisation routes was seen as having arisen through successive bottlenecks of small amplitude as the human geographic range expanded. The pattern is further interpreted as showing that subsequent migration was limited or at least specifically localised (Prugnolle *et al.*, 2005). Thus genetic diversity provides support for a single migration out of Africa.

1.5.2 Craniofacial diversity and geographic dispersal

Homo sapiens is a globally distributed species that occupies a great number of diverse environments. Although there are arguments that human craniofacial variation should be considered clinal rather than clustered into distinguishable populations (Brace, 1995), it is generally considered that human biological diversity is spatially structured (Howells, 1989). Much work has been carried out concerning the differences in craniofacial shape between geographic regions. Howells (1973, 1989, 1995) conducted extensive research on traditional craniometric data comparing global populations. His work demonstrated that human populations from distinct geographic locations can be discriminated from one another, despite the relatively restricted craniofacial morphology of humans (Relethford, 1994). Geographic differentiation has also been observed in mandibular shape (Buck and Viðarsdóttir, 2004; Nicholson and Harvati, 2006), even though the

human mandible is widely considered a poor indicator of population structure (Humprey *et al.*, 1999). Cranial measurements are moderately to strongly heritable (Devor, 1987; Sparks and Jantz, 2002) and interregional differences in craniofacial morphology are present very early in ontogeny (Viðarsdóttir *et al.*, 2002; Buck and Viðarsdóttir, 2004). The majority of research on distinguishing human populations has been carried out using traditional craniometric techniques (eg., Howells, 1989). More recently geometric morphometric techniques have been applied to the question of human regional diversity. One of the benefits of using these relatively new techniques is the objective visualisation of morphological differences (Hennessey and Stringer, 2002). In a study of four modern human groups, Hennessey and Stringer (2002) demonstrated that comparable results could be established between geometric morphometric techniques and the classic studies of Howells (1989).

Many studies of craniofacial diversity have therefore demonstrated that human populations are geographically structured and craniometric distances between populations reflect at least in part some underlying genetic differences. Relethford (2002) analysed the portioning of global variation into components that represent the relative amount of variation found among large geographic regions, among local populations within geographic regions, and within local populations. Using classic genetic markers such as red blood cell types, as well as DNA markers, he found that roughly 10% of human genetic diversity is observable among geographic regions, 5% among local populations within regions, and 85% within local populations (Relethford, 2002). He found similar results when he applied the same multivariate quantitative genetic model to cranial trait data, with approximately 13% variation among geographic regions, 6% among local populations within regions and 81% within local populations (Relethford, 2002). Thus he concluded that global craniometric variation is similar to that expected under a neutral genetic model of genetic drift balanced by gene flow. Relethford's conclusions can be taken to imply that interregionally differing selection pressures have therefore played only a limited role in producing the overall patterns of human craniometric diversity.

1.5.3 Craniofacial diversity and environmental conditions

An important question regarding the relationship between craniometric distances and their underlying genetic differences is to what extent these genetic differences are a reflection of past natural selection and/or gene flow. Just as neutral genetic markers have been used to show a good fit to the isolation by distance model on a global level (Eller, 1999), craniometric data can also be used to examine the extent to which craniometric variation is neutral or has been shaped by selection. Craniofacial morphology arises from the translation of genotype into phenotype through several epigenetic processes. The effects of environmental conditions on craniofacial shape have long been noted. In his global study of craniometric variation, Howells (1973) suggested that the separation he found between Australians and Africans on the one hand, and Europeans, Asians and Native Americans on the other, was related to the effects of climate. In an explicit search for such environmental adaptations in Howells' data, Guglielmino-Matessi and colleagues (1979) addressed the hypothesis that climate was the major environmental component responsible for the discrepancy that Howells found (Howells, 1973). The climatic data assessed were temperature, humidity and precipitation, and results found that cold stress is a factor influencing skeletal measurements (Guglielmino-Matessi *et al.*, 1979). Climatic conditions, and again the importance of cold temperature, were given as explanations for the patterns of robusticity found in Patagonian hunter gatherers from the Late Holocene (Bernal, *et al.*, 2006). In that study a correlation between craniofacial robusticity and latitude was found, suggesting an adaptation to a cold climate as a causal factor for particular morphologies such as a pronounced supraorbital ridge and glabellar region.

In reaction to Relethford's work on selection factors (1994, 2002), Roseman (2004) and Roseman and Weaver (2004) explored the effects of climatic conditions on craniofacial variation, as found in the Guglielmino-Matessi *et al.* (1979) and Bernal *et al.* (2006) studies. Roseman's results indicated that overall population history has a significant effect on the pattern of among-region differences in modern human cranial form. The results also showed, however, that differences among regions in at least some cranial features are, in part, the product of inter-regionally differing selection pressures

(Roseman, 2004). The excess differentiation that Roseman identified was most apparent in those populations living in an extremely cold environment (2004). Roseman (2004) interpreted this as the action of natural selection, associated with regional variation in temperature, resulting in some of the differences identified in cranial vault size and in aspects of nasal morphology.

1.5.4 Biomechanics and craniofacial diversity

Another environmental factor that has been documented to influence craniofacial differentiation is that of economic strategy and diet. Mechanical loading on the skull has been widely studied in relation to masticatory forces (González-José *et al.*, 2005). It has been hypothesised that reduction in masticatory muscle activity and a concomitant decrease in mechanical loading of the craniofacial skeleton induces a reduction in muscle size and their related structures. A change in economic strategy for human groups from hunting and gathering to farming and the increased processing of food would be responsible for the reduction of masticatory activity (Larsen, 1997). Processing food makes it softer and smaller in particle size, requiring less occlusal force per chew and fewer chewing cycles per unit of food (Strait, 1997). Experimental studies on non-human animals have demonstrated that diet consistency may contribute to modifications in the thickness of cortical bone and mandibular density (Bresin *et al.*, 1999). Changes in the maxillary, mandibular and palatal structures (Giesen *et al.*, 2003) and reduction in muscle size (Ciochon *et al.*, 1997) have also been noted. Masticatory forces also regulate an important portion of craniofacial growth, affecting several morphological structures such as in the brain case and sutures (Herring and Teng, 2000). Herring and Teng (2000) analysed masticatory forces in minipigs and demonstrated that the contraction of the masseter and temporalis during natural mastication caused strains in some sutures of the braincase. Minipigs move their heads during mastication and thus the neck muscles were also affected. A similar degree of coordination between concomitant mandibular and head neck movements during natural jaw activities was also reported in humans (Zafar *et al.*, 2000). This functional relationship apparently relies on common neural connections that control activities in both systems (Zafar *et al.*, 2000) so larger postneural size reported for hunter gatherers (Sardi *et al.*, 2006) may

reflect the greater masticatory activity on neck muscles which are attached to the occipital bone.

As most experimental studies have been carried out on non-human primates or other highly prognathic animals such as rodents or swine (Ciochon *et al.*, 1997), Lieberman *et al.* (2004) examined facial growth and in vivo strains generated in response to raw or dried foods versus cooked foods in a retrognathic mammal, the rock hyrax (*Procavia capensis*). It was found that in general, higher strains, as much as two fold at some sites, were generated by masticating raw versus cooked food. Significantly less growth in the ventral and posterior portions of the face, where strains are highest, was noted in hyraxes raised on cooked food. This finding resembled many of the differences evident between humans raised on highly processed rather than less processed diets and supports the hypothesis that food processing techniques have led to decreased facial growth in the mandibular and maxillary arches in recent human populations (Lieberman *et al.*, 2004). It is therefore suggested that human faces may have become relatively smaller, despite increases in body size, because of reduced levels of strain generated by chewing softer, more processed food.

The influence of economic strategy on human craniofacial morphology has also been examined in archaeological situations (González-José *et al.*, 2005; Bernal *et al.*, 2006). González-José and colleagues (2005) examined the effect of subsistence strategy on craniofacial functional components in eighteen populations of hunter-gatherers and farmers from South America. The results showed that the size and shape of the masticatory component was affected by the particular economic strategy. Two main points concerning the influence of nongenetic factors on morphological differentiation were identified; the magnitude of variation accounted for by a particular environmental force, such as the subsistence strategy of a population; and the localisation of structures which are most likely affected by this particular force. In regards to total craniometric variation, subsistence strategy proved to be of low power in differentiating between the populations. Enough differentiation was seen, however, to suggest that a proportion of variation in the morphology of the masticatory component is probably driven by either a

selective process or plastic responses during ontogeny. This led to large relative masticatory sizes prior to the transition to food production and a relaxation and consequent decrease of masticatory size after the adoption of farming (González-José *et al.*, 2005). Similar results were reported by Sardi *et al.* (2006), who again explored the craniofacial morphological consequences of the transition to food production in South America. In this study smaller craniofacial size was identified in farmers than in hunter gatherers and the functional components with the greatest variation were masticatory and posteroneural (Sardi *et al.*, 2006). Contrary to the above findings, however, are the results of a study on the variation and causal factors of craniofacial robusticity in Patagonian hunter gatherers from the Late Holocene (Bernal *et al.*, 2006). The Fueguian-Patagonian populations are considered to be among the most robust of any modern crania and biomechanical explanations have been proposed for the causes of this robusticity (Lahr and Wright, 1996). In addition to high magnitude forces due to masticatory activity resulting from a hard diet, the Fueguian-Patagonians had additional functional stress due to using the mouth as a tool (Bernal *et al.*, 2006). Bernal *et al.*, (2006) identified no association between the consumed diet and the degree of robusticity found in the crania, providing no support for a biomechanical causation. Indeed, some hunter gatherers' skulls displayed the same development of robust features as farmers' skulls. Rather, a significant correlation was found between latitude and craniofacial robusticity, with the most robust morphologies occurring at the highest latitudes. Endocrine changes related to living in a cold climate are therefore given as a possible explanation for the robust features found in these specific populations (Bernal *et al.*, 2006).

Chapter 2

Materials and Methods

2.1 Materials

2.1.1 Samples

The specimens included in this study represent 32 samples of modern humans from on and around the Indian Ocean rim. Samples were chosen to represent distinct geographic localities. Table 2.1 summarises the samples by region and country and the locations of samples shown are given in figure 2.1. Sample size is also listed in table 2.1. A maximum sample size of 35 is utilised in order to avoid the affect of discrepant sample size on the discriminant analyses. Samples smaller than 10 were only used in analyses of means. Only adult individuals are included, determined by the complete fusion of the spheno-occipital synchrondosis and by the full eruption of the permanent dentition, where available. Any crania that showed signs of disease, or bone resorption due to age, were excluded from sampling.

Figure 2.1 Locations of samples included in the study

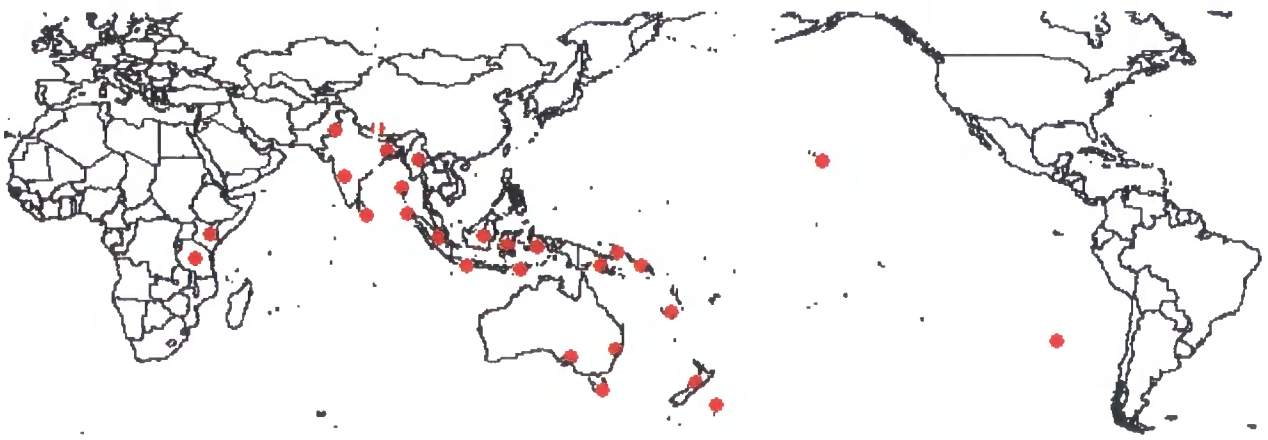


Table 2.1. Composition of data sets

Region	Country	Sample	Sample Size	Specimen Location*
Africa				
	Kenya	Teita	35	DC
	Tanzania	Haya	35	DC
South Asia				
	India	Lepcha	9	NHM
	India	Mysore	9	NHM
	India	Bengal	35	NHM, DC
	India	Punjab	35	NHM, DC
	Sri Lanka	Sri Lanka	22	NHM, O, DC
	Sri Lanka	Veddah	15	NHM
Southeast Asia				
	Myanmar	Myanmar	35	DC
	Andaman Islands	Andaman Islands	34	NHM, DC
	Nicobar Islands	Nicobar Islands	13	NHM, DC
	Borneo	Borneo	35	NHM, O, DC
	Java	Java	17	NHM, O
	Sulawesi	Sulawesi	5	NHM
	Moluccas	Moluccas	6	NHM
	Sumatra	Sumatra	6	NHM, DC
	Timor	Timor	7	NHM
New Guinea				
	New Guinea	Awaiama	19	DC
	New Guinea	Kwaiawata	18	DC
	New Guinea	Sinaugolo	21	NHM, DC
Melanesia				
	New Britain	New Britain	35	NHM, DC
	Solomon Islands	Solomon Islands	21	NHM, O, DC
	Louisiade Archipelago	Louisiade Archipelago	10	NHM, O

	New Caledonia	New Caledonia	15	NHM, DC
	Loyalty Islands	Loyalty Islands	7	NHM
Australia				
	Australia	New South Wales	24	NHM, O, DC
	Australia	South Australia	16	NHM, O, DC
	Australia	Tasmania	12	NHM, O
Polynesia				
	Easter Island	Easter Island	29	NHM
	Chatham Islands	Chatham Islands	35	NHM, DC
	New Zealand	New Zealand	21	NHM
	Hawaii	Hawaii	8	NHM, O
Total			**708**	

* NHM, Natural History Museum, London; O, The University Museum of Natural History, University of Oxford: DC, The Duckworth Laboratory, University of Cambridge.

Sample provenance

The amount of data available for the provenance of the different samples varies considerably. A summary of what is known of the provenance for each sample, grouped by region, is given below.

Africa

Two African samples are included in the present study, the Teita of Kenya and the Haya from Musira Island, Tanzania.

South Asia

Four samples from India and two samples from Sri Lanka are included. The samples from South Asia are taken from distinct geographic locations, with the exceptions of the Lepcha and Veddah. The Bengal sample comes from the northeast region of India and the Punjab sample from the northwest. The Sri Lanka sample is made up of a mix of Singhalese and Tamils who have been shown in unpublished work to be morphologically indistinguishable. The tribal samples consist of the Veddah from Sri Lanka and the Lepcha from Sikkim. The Lepcha are a tribe inhabiting northern India and are believed to be the descendents of Mongols who migrated into India from North Asia during the seventeenth century (Risley, 1891). The Veddah of South Asia are thought to be the indigenous tribe of Sri Lanka, biologically distinct from the Sinhalese and Tamil groups (Bulbeck, 2003; Deraniyagala, 1992).

Southeast Asia

The nine Southeast Asian population samples each represent distinct geographic locations. The Andaman Islands sample consists of individuals from both Great and South Andaman.

New Guinea and Melanesia

The five Melanesian samples are taken from distinct geographic locations. The Awaiama sample was collected from the Awaiama bay region of New Guinea and the Sinaugolo sample from the neighbourhood of Taberogoro, near Port Moresby, New

Guinea. The Kwaiawata sample was collected from the Kwaiawata Island adjacent to the South West tip of New Guinea.

Australia

The three Australian samples are made up of specimens collected in the general areas of South Australia, New South Wales and Tasmania.

Polynesia

The Polynesian samples include a Maori sample from various locations on New Zealand, a Moriori sample from the Chatham Islands, an Easter Island sample and a sample from Oahu, Hawaii.

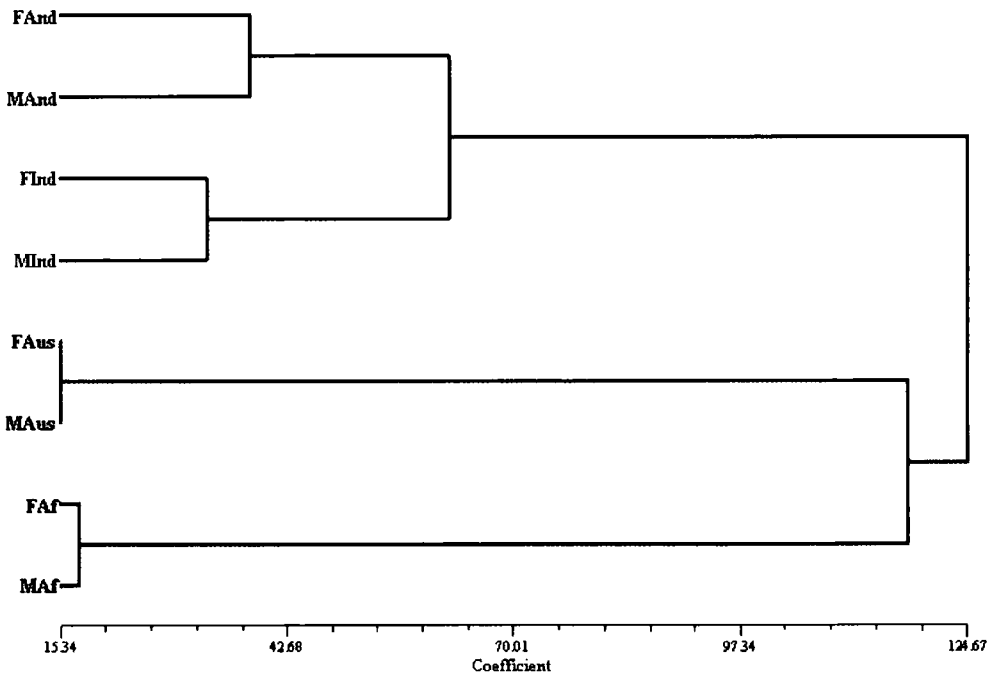
No attempt was made to sex individuals and mixed sex samples are used throughout. To test that it is possible to use mixed sex samples, an analysis was undertaken of four population samples of which sexed individuals were available. These samples are from the Andaman Islands, Australia, India and Africa. Table 2.2 gives the results of the crossvalidation analysis. For each sample, the individuals were almost always placed in either the male or female group from their original population. A phenogram produced from the Mahalanobis' distances between the sample populations is illustrated in figure 2.2. It is clear that the male and female of each population are more similar to one another than they are to members of the same sex from a different population. Therefore mixed sex samples are demonstrated to be adequate for these analyses as inter population differences are greater than those between sexes.

Table 2.2 Cross validation analysis: sexed groups

FAnd, Female Andaman Islands; MAnd, Male Andaman Islands; FAus, Female Australian; MAus, Male Australian; FInd, Female Indian; MInd, Male Indian; FAf, Female African; MAf, Male Africa.

	FAnd	MAnd	FAus	MAus	FInd	MInd	FAf	MAf	Total
FAnd %	**83.33**	**16.67**	0.00	0.00	0.00	0.00	0.00	0.00	100.00
MAnd %	**33.33**	**33.33**	0.00	0.00	0.00	0.00	16.67	16.67	100.00
FAus %	0.00	0.00	**42.86**	**50.00**	0.00	0.00	7.14	0.00	100.00
MAus %	0.00	0.00	**42.86**	**57.14**	0.00	0.00	0.00	0.00	100.00
Find %	8.33	8.33	0.00	0.00	**58.33**	**25.00**	0.00	0.00	100.00
MInd %	0.00	16.67	0.00	0.00	**8.33**	**75.00**	0.00	0.00	100.00
FAf %	0.00	0.00	0.00	0.00	0.00	0.00	**56.25**	**43.75**	100.00
MAf %	0.00	0.00	0.00	0.00	0.00	0.00	**43.75**	**56.25**	100.00

Figure 2.2 Phenogram showing relative shape relationships between the sexed groups



2.2 Methods

2.2.1 Landmark data

The data were collected in the form of three-dimensional landmarks coordinates using a Microscribe 3DX desktop digitizing system (Immersion Corporation San Jose, C.A.). Forty seven unilateral landmarks were selected to allow a good representation of craniofacial morphology (table 2.3). The use of unilateral landmarks has been shown to give similar results with respect to patterns of variation as do bilateral landmarks and allows the available sample to be maximised whilst retaining morphological information from the entire craniofacial skeleton (Viðarsdóttir and O'Higgins, 2001).

Landmarks are anatomically definable points on a specimen that represent its shape. The use of landmark data in morphological shape analyses requires that landmark points must be biological loci that can be clearly defined and reliably located. There are practical difficulties in identifying anatomical landmarks, however, and a taxonomic system exists to classify the relative homology (Bookstein, 1991; O'Higgins, 2000):

Type I Landmarks - The landmark homology is supported by the strongest local evidence, such as the crossing of the sagittal and coronal sutures.

Type II Landmarks - The landmark homology is supported by geometric evidence, such as the extreme point on the curvature of a facet.

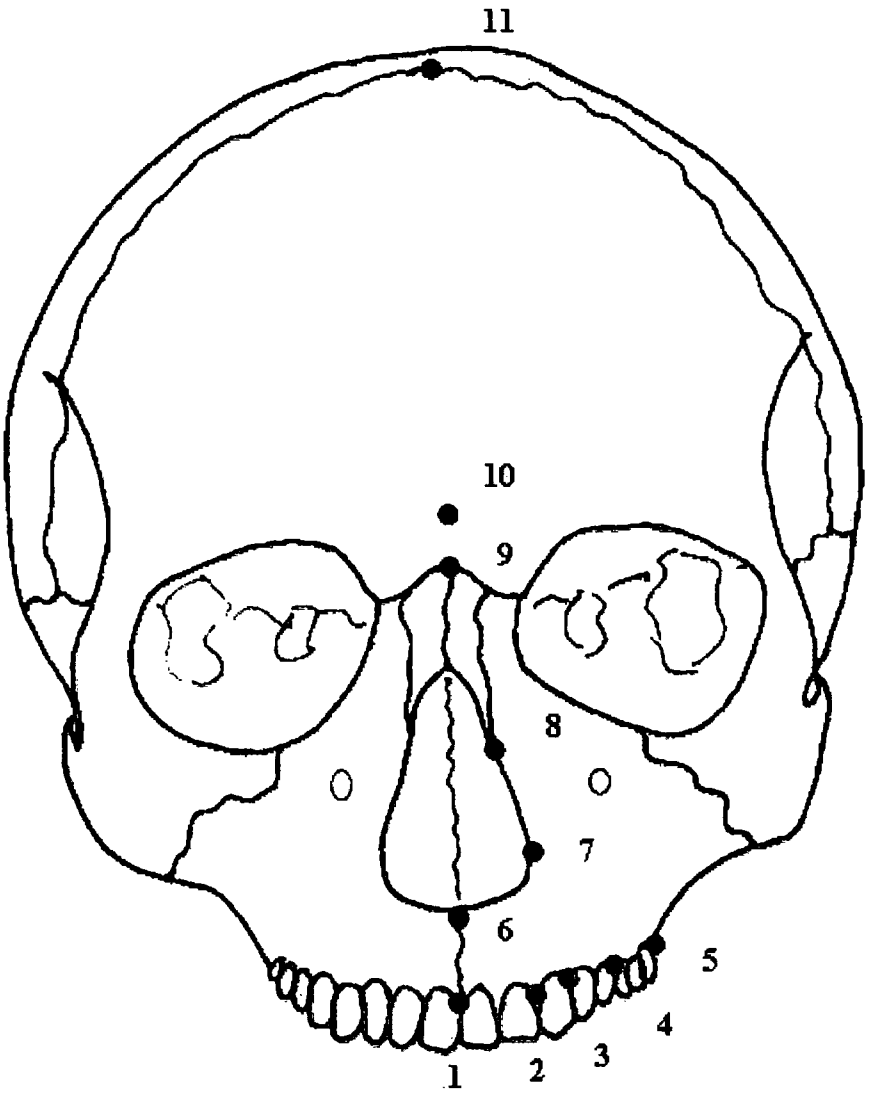
Type III Landmarks - The landmark can be reliably located to an outline or surface, but not at a specific location, such as the most inferior point on the femoral head.

Table 2.3 Craniofacial landmarks

Anterior view

Number	Description
1	Midline point at the most anterior point on the alveolar process of the maxilla
2	Mid point between the canine and the second incisor on the alveolar process of the maxilla
3	Mid point between the canine and the first premolar on the alveolar process of the maxilla
4	Mid point between the second premolar and the first molar on the alveolar process of the maxilla
5	Most posterior point on the alveolar process of the maxilla
6	Point where a line tangent to the most inferior points of the two curves of the inferior nasal aperture margin crosses the midline
7	Most lateral point on the margin of the nasal aperture
8	Most inferior point where the nasal bone and the maxilla intersect
9	Midline point where the two nasal bones and the frontal intersect
10	Most anterior midline point on the frontal bone
11	Ectocranial point where the coronal and sagittal sutures intersect

Figure 2.3 Landmarks: Anterior view

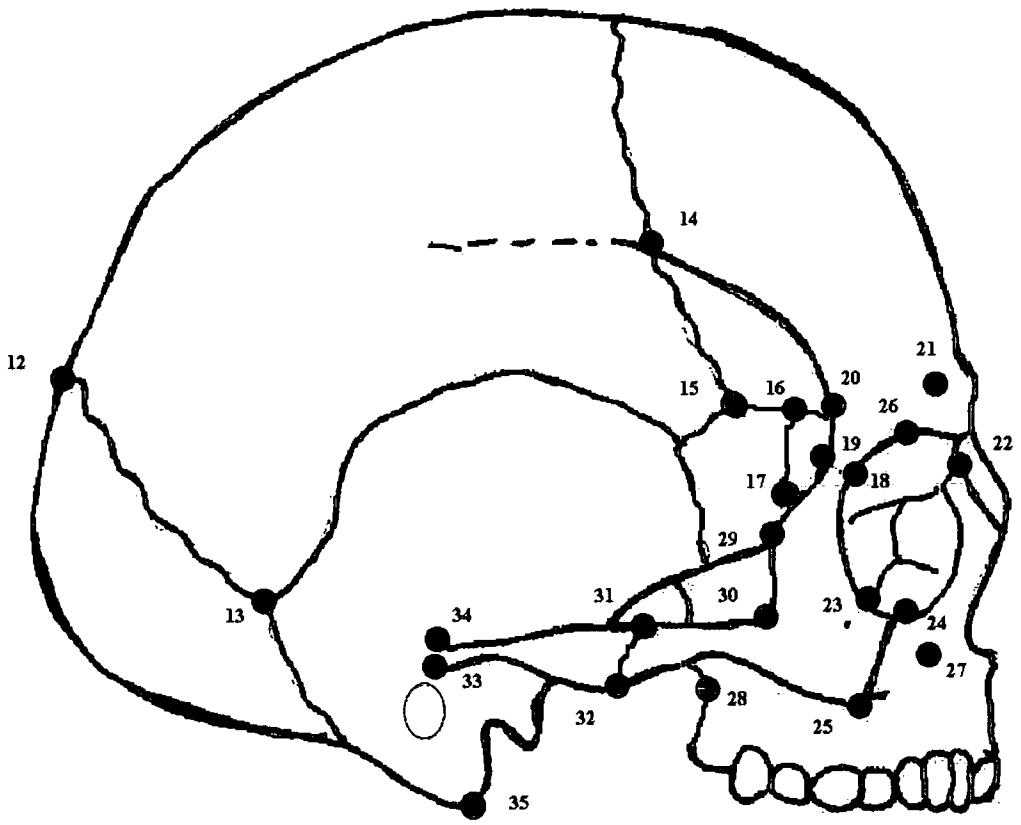


Lateral view

Number	Description
12	Ectocranial midline point where the sagittal and lambdoidal sutures intersect
13	Point where the lambdoidal, parietomastoid and occipitomastoid sutures meet
14	Point where the coronal suture crosses the temporal line
15	Point where the coronal suture intersects with the superior edge of the sphenoid
16	Point of intersection between the zygomatic, sphenoid and frontal
17	Most inferior point of intersection between the zygomatic and the sphenoid
18	Point where the frontozygomatic suture crosses the inner orbital rim
19	Point where the frontozygomaric suture crosses the outer orbital rim
20	Point where the temporal line reaches its most anteriomedial position on the frontal
21	Most anterior point on the superciliary arch
22	Most superior point where the nasal bone and the maxilla intersect
23	Most inferior and most lateral point on the orbital margin
24	Point where the orbital rim intersects with the zygomaticomaxillary suture
25	Most inferior point on the zygomaticomaxillary suture
26	Point at which a horizontal line drawn from 25. intersects with the orbital rim
27	Most superior point on the infraorbital foramen
28	Most superior and medial point on the lateral edge of the maxilla
29	Point of maximum lateral extent of the lateral surface of the zygomatic arch

30	Point in the depth of the notch between the temporal and frontal processes of the zygomatic
31	Most superior point on the intersection between the zygomatic and the temporal
32	Most inferior point on the intersection between the zygomatic and the temporal
33	Uppermost point on the margin of the external auditory meatus
34	Point vertically above the centre of the external auditory meatus at the root of the zygomatic process
35	Most inferior point on the mastoid process

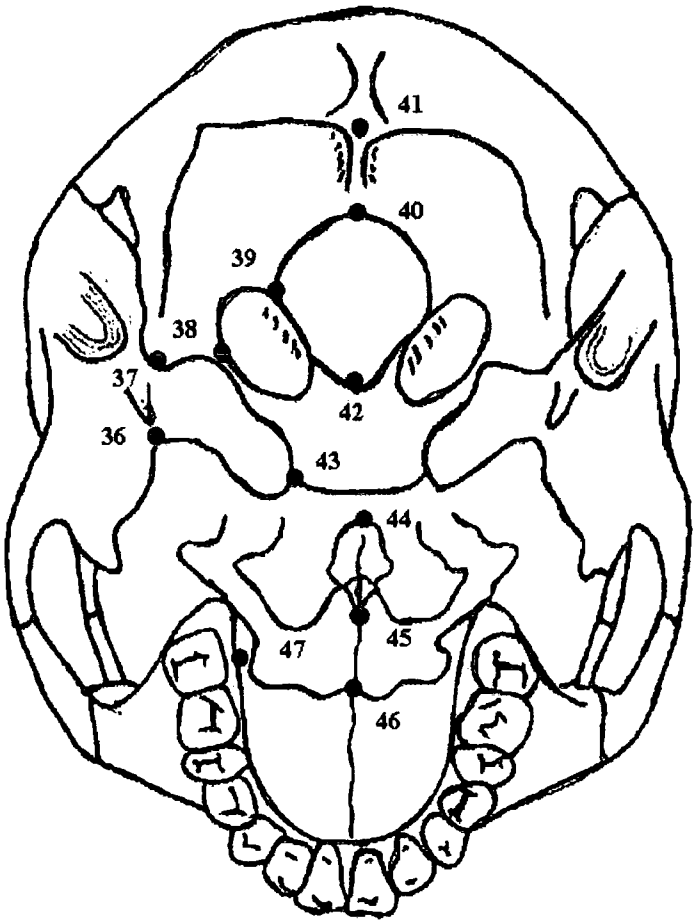
Figure 2.4 Landmarks: Lateral view



Inferior view

Number	Description
36	Most anterior point on the intersection between the sphenoid and temporal
37	Most lateral point on the jugular process of the occipital
38	Point of intersection of the occipital condyle with the jugular process
39	Point of intersection of the occipital condyle with the lateral margin of the foramen magnum
40	Midline point at the posterior margin of the foramen magnum
41	Point at which the superior nuchal lines merge in the external occipital protuberance
42	Midline point on the anterior margin of the foramen magnum
43	Most posterior midline point on the vomer
44	Most lateral and anterior point on the occipital
45	Point on the interpalatal suture where a line drawn between the deepest parts of the notices at the rear of the palate crosses the midline
46	Most anterior point on the interpalatal suture
47	Most anterior point on the lesser palatine foramen

Figure 2.5 Landmarks: Inferior view



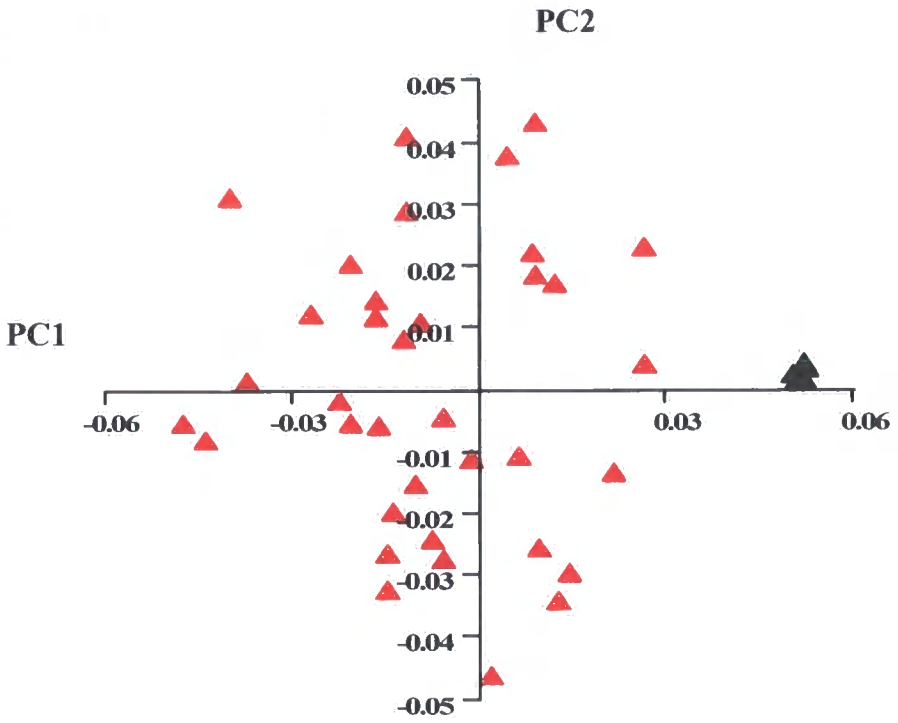
2.2.2 Data collection and accuracy

The three-dimensional landmarks were collected from the side of the cranium that displayed the best preservation. The cranium to be measured is aligned so that all landmarks can be collected in one sitting and secured so that no movement can take place during measurement. The Microscribe digitiser works by recording the location of the tip of the stylus. By placing the stylus on the predetermined landmark, the x, y, z coordinates of the landmark are transferred to an Excel spreadsheet (© Microsoft Corporation). The digitiser has an accuracy of 0.009" (Immersion Corporation San Jose, C.A.).

2.2.3 Precision of measurement

Error is assessed by measuring a randomly selected cranium five times, then combining these five shapes with 36 crania from the same sample population, as per O'Higgins and Jones (1998). The combined sample is submitted to Procrustes registration and principal components analysis (PCA). The PCA of the registered shapes is presented in figure 2.6. It is evident from the PCA results that the five repeats, in black, form a close grouping with each other on both PC1 (15.9% of the variance) and PC2 (10.8% of the variance). The five repeats also group closely together on each of the remaining PC axes. It is also evident that the spread of the five repeats is consistently smaller than that for the population sample. Thus any error between the repeat specimens is considerably smaller than those intra population differences observed.

Figure 2.6 Precision of measurement



2.2.4 Data analysis

2.2.4.1 Geometric morphometrics

This study uses geometric morphometric techniques, to analyse craniofacial variation within and between the sample populations. Geometric morphometrics provides certain advantages over traditional craniometric techniques, both methodologically and statistically (Ousley and McKeown, 2001). Conventional morphometric studies are based upon multivariate analyses of arbitrary collections of distance measurements (Rohlf, 1999). Thus, only part of the information that could be obtained from the positions of biological landmarks is gained, as these methods do not take into account the spatial relationships among the measured variables. By using three-dimensional analytical techniques, geometric morphometrics represents an advance because it allows for the measurement of variation between shapes and the elucidation of the properties of multidimensional shape space (Rohlf, 1999). Geometric morphometric techniques are also advantageous in that the geometry of the study object is better preserved in the data at each stage of the analysis. It is possible to identify the landmarks where shape variation occurs, as well as the relative levels of variation at each landmark (Rohlf and Marcus, 1993; O'Higgins, 2000).

2.2.4.2 General Procrustes analysis

The digitised coordinates are superimposed using Generalised Procrustes analysis (GPA) in *morphologika* (© Paul O'Higgins and Nicholas Jones, University College London). Procrustes based registration methods do not introduce bias into the distribution of specimens where landmarks vary independently, and have been shown to have highest statistical power in practical applications (Rohlf, 1999, 2000). GPA registers series of forms by removing translational, rotational and reflected differences, and scales them according to centroid size. Centroid size is the square root of the sum of squared distances of all landmarks to the centroid of the object (Dryden and Mardia, 1998). The centroid is described as being the mean of all landmarks for a shape (O'Higgins and Jones, 1998). Centroid size is the measure of size used in this study as it is the only size measure that is considered statistically independent of the shape of a landmark

configuration (Dryden and Mardia, 1998; O'Higgins and Jones, 1998). Once specimen forms have been scaled they are referred to as shapes.

Registered landmark configurations can be represented as points in a shape space which is of lower dimensionality than the figure space (=km dimensions; k = number of landmarks, m = real dimensions), since location (m dimensions), rotation (m(m-1)/2 dimensions) and scale (1 dimension) differences have been removed (O'Higgins and Jones, 1998). This is known as Kendall's shape space (Kendall, 1984), or more recently as Procrustes shape space. The shape space is non-Euclidian and therefore the data is projected into the linear tangent space to allow the use of standard multivariate analysis (Dryden & Mardia, 1993; Kent 1994). Rohlf (1996) states that in biological applications the approximation of tangent space is justified when there are more than just a few landmarks (Rohlf, 1996). The use of the tangent space projection allows for the use of standard multivariate techniques to explore the statistical relationship between different specimens. GPA is performed in this study using *morphologika* (© Paul O'Higgins and Nicholas Jones, University College, London).

2.2.4.3 Principal components analysis

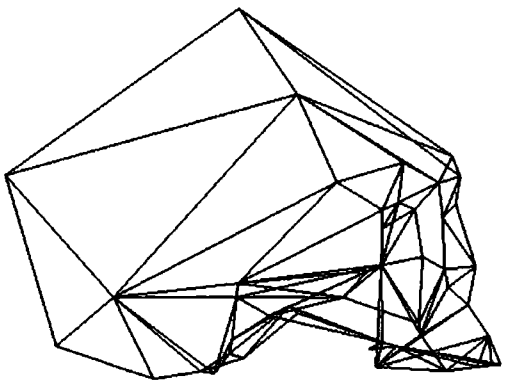
The registered landmark coordinates are analysed using principal components analysis (PCA) in order to explore how the variation is partitioned within and among the samples (Mardia *et al.*, 1979). PCA is a descriptive measure that employs the pooled variance-covariance structure of the total data set without regard for the geographic origin of the samples. This technique makes no prior assumption of dependence of one variable upon another and each observation is represented by a point in multidimensional space. Together the observations form a hyperdimensional cloud. PCA describes the hyperdimensional cloud by calculating the principal axes of variation through it, known as principal components (PCs). The first principal component (PC1) represents the line that passes through the centroid and minimises the square of the distance of each observation to that line. PC1 thus explains the largest amount of variance found in the data. The second component provides the next largest amount and so on. The proportion of variance accounted for by individual PCs is given by associated

eigenvalues. All PCs are orthogonal to each other and are therefore statistically independent. The majority of variance within the sample will often be described by a relatively small number of PCs and thus the dimensionality of the data set is reduced. PCAs are carried out using *morphologika* (© Paul O'Higgins and Nicholas Jones, University College, London).

2.2.4.4 Visualisation

Geometric morphometric techniques allow for shape change to be readily visualised. As the landmark geometry of a shape is preserved following GPA, a mean shape can theoretically be constructed. This mean shape (i.e. the shape at the centroid) corresponds to the zero point on the x and y axes and can be warped to represent hypothetical shapes at different points within the PCA. An informative 'morphing' animation of shape variation can be produced which provides information on how shape change between specimens occurs. The mean shape can be visualised by constructing triangular polygons between sets of landmarks, so as to build up a wireframe model of the landmark configuration (figure 2.7).

Figure 2.7 Wireframe representation of the craniofacial skeleton



2.2.4.5 Thin plate splines

Visualisations can be further interpreted using Cartesian transformation grids (Thompson, 1917) calculated from triplets of thin-plate splines (TPS) (Bookstein, 1989).

Grids derived from TPS indicate how the space surrounding a reference shape might be deformed into that surrounding a target shape, such that landmarks on the reference shape morph exactly into those of the target. The TPS ensure that the deformations involve minimum bending energy (Bookstein, 1989) and are completely registration free. Statistical and graphical models of shape transformations that result from these approaches are readily interpretable and highly visual. The computation of transformation grids using thin plate splines in this study, is performed using *morphologika* (© Paul O'Higgins and Nicholas Jones, University College, London).

2.2.4.6 Mahalanobis' D^2 distances

Mahalanobis' D^2 distances are obtained for the samples included in the analysis. Mahalanobis' D^2 is a measure of shape differences between groups taking into consideration the variance and covariance among populations. Mahalanobis' D^2 distances are calculated using SAS (The SAS Institute Inc., 1996).

2.2.4.7 Procrustes distances

Procrustes distances are used to calculate the distance between the mean shape of each sample. Procrustes distances measure the degree of fit between the sample means following Procrustes registration. The distance is approximately the square root of the sum of squared distances between the positions of the landmarks following Procrustes registration (Kendall, 1984). Procrustes distances are calculated using Procrustes distances.exe (© Paul O'Higgins, University College, London).

2.2.4.8 Discriminant analysis with crossvalidation

Discriminant analysis with crossvalidation is used to classify individuals into predefined groups, based upon Mahalanobis' D^2 distances. Each individual is assigned a probability of belonging to a given group based on the distance of its discriminant function from that of each group mean. Crossvalidation is employed as it provides a better assessment of classification accuracy than standard discriminant analysis. During crossvalidation, classification is carried out for each individual in turn and the discriminant function used in each case is constructed with that individual removed.

Every individual is therefore reclassified as if it were an unknown specimen, providing a more conservative assessment. The crossvalidation analyses are carried out using SAS (The SAS Institute Inc., 1996).

2.2.4.9 UPGMA

Phenograms are generated to illustrate the morphological relationships between groups using the unweighted pairgroup method using arithmetical averages (UPGMA) clustering strategy. This technique calculates the average similarity or dissimilarity of a candidate individual to an existing cluster, giving each individual in that cluster equal weighting. It then calculates a new distance matrix, using the arithmetical average of the existing clusters as a basis for calculating the new distances. This is repeated after each step until all the clusters are joined. The phenogram is only a two dimensional representation of the actual multidimensional relationships between the groups being analysed. It is therefore not a fully accurate depiction of the relationships being explored but remains a useful comparative tool showing a possible reconstruction of shape relationships. The UPGMA cluster analyses are carried out using the NT-Sys program (Applied Biostatistics Inc., 1989).

2.2.4.10 Tests of correlation

Correlation analysis, a measure of the association between two variables is undertaken using Pearson's correlation coefficient (r) and associated p-value (Zelditch et al, 2004). Values are calculated using the statistical software package SPSS (SPSS for Windows, Rel. 14.0.2. 2006. Chicago: SPSS Inc.).

2.2.4.11 Geographic distances

Geographic distances between sample locations are measured by two methods. Minimum distances between the sample locations are calculated using latitude and longitude coordinates. Coordinates correspond to a stated geographic point of origin for the sample or from a central location where the exact source of the sample is not known. Distances are calculated using the website http://www.go.ednet.ns.ca/~larry/bsc/jslatlng.html created by Larry Bogan and last

accessed on 2nd February 2007. The calculation uses the ellipsoid of the Earth, flattened by 1 in 298 with an equatorial radius of 6378.14 km. For estimated coastal route distances a distance calculator tool from the 3D World Atlas CD Rom (Dorling Kindersley, 2002) is used. Geographic distances are recorded in kilometres.

2.2.4.12 Climatic data

The following independent variables are used in Chapter 3: mean annual high temperature, mean annual low temperature and total annual precipitation. In all statistical procedures, the mean annual temperatures are presented in degrees Celsius, and the annual sum of precipitations in cm. The climatic data are derived from the Weatherbase data base on www.weatherbase.com, collected on 22/08/05. For samples where the localised place of origin is known, for example the Teita sample, data is taken from the nearest weather station. For samples that represent an assortment of specimens from a larger geographic region, such as the Sri Lanka sample, data is taken from a weather station situated at the approximate centre of the geographic distribution. It must be noted that the climatic data included in this study is that of the present day, which may differ to that of when the individuals included in this study were alive.

Chapter 3

Craniofacial Diversity around the Indian Ocean Rim

3.1 Introduction

Any attempt to elucidate the evolutionary history of *Homo sapiens* must take into account the extent to which human morphological variation is geographically structured. Lahr (1996) identified craniofacial diversification in *Homo sapiens* as being closely linked to the process of geographical dispersal and expansion from a single ancestral source. In order to examine the phylogenetic processes of modern human evolution, it is therefore important to look at morphological variation on a cross regional scale. This chapter is concerned with identifying and exploring the patterns of craniofacial diversification found between modern populations located on and around the Indian Ocean rim.

The diversity of the human craniofacial skeleton is well known from previous studies using both traditional craniometric measurements and the geometric morphometric techniques employed in the present study (Falk and Corruccini, 1982; Howells, 1989; Hanihara, 1996; Lahr, 1996; Relethford, 1994; Viðarsdóttir *et al.*, 2002). Hanihara (1996), for example, used 23 traditional craniometric measurements to compare the craniofacial features of populations from major geographical areas of the Old World. He found that patterns of craniofacial variation are not necessarily consistent with the geographical distribution of the populations studied. Australians, for example, were said to show closer similarities to African populations than to Melanesians, their geographic neighbours (Hanihara, 1996). Viðarsdóttir *et al.* (2002) applied geometric morphometrics to the regional differences in the ontogeny of the facial skeleton and concluded that modern human populations can be distinguished on the basis of facial shape alone. Within the studies of craniofacial diversity, work has also been undertaken to explain the morphological diversity of *Homo sapiens* in an evolutionary framework. Howells (1989), for example, demonstrated that the craniofacial differences found between modern populations are small in relation to the differences found between the

same modern populations and Neanderthals. Relethford (1994) and Relethford and Harpending (1994) also identified small amounts of morphological variation between human populations, showing that such variation was comparable in degree to genetic variation. Hanihara *et al.* (2003) attempted to characterise global biological diversity by undertaking a large scale analysis of discrete cranial traits of 70 different populations. This study also found similar patterning between genetic and morphological diversity and that clinal relationships exist between regional groups. Lahr (1996) undertook a study of cranial diversity to explicitly review the Multiregional versus the Recent African Origin hypotheses, concluding that regional differences in modern human populations can be explained by the latter.

The route of the initial geographic expansion of *Homo sapiens* out of Africa along the Indian Ocean rim will have played an important role in the establishment of such morphological diversification. The aim of this chapter is therefore to obtain information from present day patterns of human diversity to help discern issues of human evolution, specifically the migration of *Homo sapiens* around the Indian Ocean rim. Patterns of craniofacial diversity will be assessed in relation to shape and size and any similarities and differences in craniofacial shape between the populations will be identified.

Hypotheses

H_1 "There are no differences in craniofacial shape between geographically distinct populations from around the Indian Ocean rim"

H_2 "There are no differences in craniofacial size between the distinct populations from around the Indian Ocean rim"

H_3 "There is no statistically significant relationship between craniofacial shape differences and centroid size in the populations from around the Indian Ocean rim"

3.1.1 Shape variation and geographic distance

Having identified the patterns of diversity around the Indian Ocean rim, this chapter will explore whether these patterns can be explained specifically by the southern route hypothesis. It is known that craniofacial shape variation is in part dictated by geography (Konigsberg, 1990; González-José *et al.*, 2001). A number of studies have found that population spatial separation is one of the most dominant influences on the degree and pattern of craniometric differentiation. Konigsberg (1990), noted that in most anthropological studies there is a positive relationship between increasing geographic separation and phenotypic distance among groups. In a study of cranial metric and discrete trait variation in the Terminal Late Archaic of Ohio, for example, Sciulli (1990) found that although all the samples from the period were shown to be related, those most geographically near to one another were more closely related than distant samples. Regarding the settlement of Patagonia, González-José *et al.* (2001) also found that biological distance was strongly associated with spatial separation, with a strong and highly significant correlation between geographic and nonmetric cranial distances. Lalueza *et al.* (1996) similarly proposed that geographic distance is the main factor influencing the differentiation, from a single ancestral population, of human groups from Tierra del Fuego and Patagonia.

Hypotheses

Geographic barriers such as rivers, oceans and mountains divide the earth into varied regions which may impede migration and the interaction of separate populations, thus creating regional clines. The tendency for more variation to occur among regional populations than among local populations within regions is a reflection of the isolation by distance model (Relethford, 2002). Wright (1931) noted that isolated populations tend to diverge from one another as a result of genetic drift and that the pattern of divergence among populations reflects the extent of migration between them. Geographic signalling may thus be prevalent due to isolation by distance and/or past population movements being reflected in the craniofacial similarities within regions. In order to test for the effects of geographic signalling on craniofacial shape diversity, therefore, the following null hypothesis is erected:

H_4 "Relationships in craniofacial shape are not determined by geographic signalling"

The effects of geographic proximity as the determinant of craniofacial shape variation will be tested by two different methods. Shape variation as described by the principal components will be correlated against the latitudinal and longitudinal coordinates of the location of each of the populations. Secondly, the biological distances, as described in section 3.3, will be correlated against two measures of geographic distance. These measures of geographic distance will be calculated in two differing ways, firstly using direct distances between the sample locations. These minimum distances are calculated using the latitude and longitudinal coordinates of the central location of the representative samples. The second set of geographic distances are calculated to represent the distances between the samples taking the postulated coastal route, giving a larger distance between the samples (section 3.3 provides a detailed explanation of the calculations). The hypothesis will be refuted if there is no correlation of either measure of shape variation with geographic distance.

3.1.2 Shape variation and migration out of Africa

Support for the recent African model is given by the observation that African populations are the most genetically diverse across the world and non-Africans carry only a fraction of the genetic diversity that is currently present in African populations (Tishkoff and Kidd, 2004). Two recent studies exploring the relationships between genetic diversity and geographic distance give further support to the Out of Africa hypothesis (Prugnolle *et al.*, 2005; Ramachandran *et al.*, 2005). Prugnolle *et al.* (2005) demonstrated that genetic distance from East Africa, along likely colonisation pathways such as that around the Indian Ocean rim, is an excellent predictor for genetic diversity of human populations ($R^2 = 85\%$). Taking Ethiopia as a point of origin, a strong negative correlation was found between geographic distance to East Africa and genetic diversity. Populations most geographically distant from East Africa were characterised by the lowest genetic variability. Similarly, Ramachandran *et al.* (2005) found a linear

relationship between genetic and geographic distance in a worldwide sample of human populations. Differing global locations were considered as possible sources of the human expansion, but no geographic origin outside of Africa accounted as well for the observed patterns of genetic diversity found in the samples (Ramachandran *et al.*, 2005). In a combined study of genetics and morphology, Relethford (2004b), found that a common pattern of global gene flow, mediated by geographic distance, is detectable in diverse genetic and morphological data. An alternative explanation proposed by Relethford (2004b) for these findings was that the correspondence between genetic similarity and geographic distance reflects the history of dispersal of humans out of Africa.

Hypotheses

The above studies suggest that it is possible to determine traces of the original Late Pleistocene migration around the Indian Ocean rim through genetic diversity of modern populations. This chapter will therefore further address whether similar traces of the original migration are present in the craniofacial skeletal shape of the modern populations around the Indian Ocean rim. Geographic distance from Africa will be correlated against the biological distance of each population from Africa, as represented by the Procrustes distances between the means of the groups, as calculated in Chapter 3. The two measures of geographic distance described above will be used. The isolation by distance model (Wright, 1943) predicts that genetic or phenotypic similarity will decrease exponentially with increasing geographic distance between populations. In particular, individuals belonging to the source population are expected to be more similar to one another than are individuals from different geographic regions (Song *et al.*, 2006). The above mentioned molecular studies (Prugnolle *et al.*, 2005; Ramachandran *et al.*, 2005) demonstrate that the genetic diversity patterns of modern humans fit well with models of isolation by distance. Under a fixed migration pattern, incorporating the isolation by distance model, there may also be positive correlation between phenotypic distance and spatial distance. It is thus predicted that populations geographically nearer to Africa would be more similar in craniofacial morphology and those more distant would be more dissimilar. The following null hypothesis is erected:

H_5 "Craniofacial shape diversity is not determined by distance from Africa"

Hypothesis 5 will be refuted if there is a correlation between geographic distance from Africa and biological distance, as represented by the Procrustes distances between the means of the populations.

3.2 Materials

The materials in this study represent sub-sets of extant populations that are found on and around the Indian Ocean rim. The samples consist of mixed sex specimens (see Chapter 2). Table 3.1 summarises the sample sizes for each population. In order to understand craniofacial morphological diversity among the samples around the Indian Ocean rim, variation is estimated using regions and samples from local populations as units of analysis. To fully explore the nature of morphological diversity found in modern populations, several sub-populations from a single country have been included where possible. In the present chapter, four groups from India and Sri Lanka have been included, three groups from New Guinea and two groups from Australia (table 3.1). Further details of the provenance of these specimens, assessment of maturation and determination of inclusion can be found in the materials section of Chapter 2.

Table 3.1 Indian Ocean rim: Composition of data sets

Region	Country	Sample	Sample Size	Specimen Location*
Africa				
	Kenya	Teita	35	DC
	Tanzania	Haya	35	DC
South Asia				
	India	Bengal	35	NHM, DC
	India	Punjab	35	NHM, DC
	Sri Lanka	Sri Lanka	22	NHM, O, DC
	Sri Lanka	Veddah	15	NHM
Southeast Asia				
	Myanmar	Myanmar	35	DC
	Andaman Islands	Andaman Islands	34	NHM, DC
	Nicobar Islands	Nicobar Islands	13	NHM, DC
	Borneo	Borneo	35	NHM, O, DC
	Java	Java	17	NHM, O
Melanesia				
	New Guinea	Awaiama	19	DC
	New Guinea	Kwaiawata	18	DC
	New Guinea	Sinaugolo	21	NHM, DC
	New Britain	New Britain	35	NHM, DC
	Solomon Islands	Solomon Islands	21	NHM, O, DC
	New Caledonia	New Caledonia	15	NHM, DC
Australia				
	Australia	New South Wales	24	NHM, O, DC
	Australia	South Australia	16	NHM, O, DC
	Australia	Tasmania	12	NHM, O
TOTAL			**492**	

* NHM, Natural History Museum, London; O, The University Museum of Natural History, University of Oxford: DC, The Duckworth Laboratory, University of Cambridge.

3.3 Methods

As discussed in Chapter 2, all OTUs are Procrustes registered to remove translational, rotational and size differences before being analysed. Principal components analysis is conducted on the Procrustes registered coordinates. Individual specimen centroid size, prior to GPA, is retained and used in this study as an expression of the overall scale of the landmark configuration (Viðarsdóttir and O'Higgins, 2003). Shape differences along the PCs are visualised by warping the triangulated surface of the mean shape to represent shapes at any position within the plot, using the loadings of original landmark coordinates on these PCs (O'Higgins and Jones, 1998). Thin Plate Splines (TPS) are further utilised to visualise shape differences in greater detail.

Biological Distances

The degree of differentiation in shape between the groups is measured using the discriminant function of Mahalanobis' D for the complete samples. Mahalanobis' D, or generalised distance, is a function of the group means and the pooled variances and covariances among populations. Mahalanobis' D is used to test whether group centroids are significantly different. The Mahalanobis distances are calculated using SAS (The SAS Institute Inc., 1996). To measure the differences between the means of population samples, Procrustes distances are utilised. The distance is approximately the square root of the sum of squared differences between the positions of the landmarks after GPA (Kendall, 1984). Procrustes distances are calculated using the executable Procrustes distances.exe (P.O. Higgins, University College London).

Discriminant Analysis

Discriminant analysis with crossvalidation is used to classify individuals into predefined groups, based upon Mahalanobis' D distances. Each individual is assigned a probability of belonging to a given group based on the distance of its discriminant function from that of each group mean. Crossvalidation is employed as it provides a better assessment of classification accuracy than standard discriminant analysis. During crossvalidation, classification is carried out for each individual in turn and the discriminant function used

in each case is constructed with that individual removed. The crossvalidation analyses are carried out using SAS (The SAS Institute Inc., 1996).

Distance Phenograms

UPGMA phenograms are constructed using the Mahalanobis' and Procrustes distances, in order to summarise the morphological relationships between the groups. The phenograms are created using the program NTSYS (Exeter Software).

Correlations

In order to investigate whether any correlation exists between centroid size and scores on any one PC, Pearson's correlation coefficient (r) and associated p-value are calculated using the statistical software package SPSS (SPSS for Windows, Rel. 14.0.2. 2006. Chicago: SPSS Inc.).

Geographic distance

Two measures of geographic distance are calculated, the shortest geographic distance between population locales, and distance along shorelines. Minimum linear distances between the samples are obtained by calculating the distance between the latitude and longitude coordinates of any two samples. The data were obtained using an online calculator found at http://www.go.ednet.ns.ca/~larry/bsc/jslatlng.html on 22/08/05. This calculator uses the ellipsoid of the Earth, flattened by 1 in 298 with an equatorial radius of 6378.14 km. Coastal route distances are estimated using the distance calculator tool from the 3D World Atlas CD Rom (Dorling Kindersley, 2002). This tool measures the length of the coastlines and sea crossings where applicable between any two sample localities. Distances are calculated from the central locale of the origin of the samples. All distances are expressed in kilometres between the pairs of localities.

3.4 Results

3.4.1 Craniofacial shape variation between groups

In order to assess the degree of differentiation in shape between the samples, principal components analysis is conducted on the Procrustes fitted data of the twenty sample populations. There is no separation of the samples on any single PC, as illustrated by the PCA graph of PC1 versus PC2 (figure 3.1). The principal components scores for the complete sample variance are given in table 3.2. PC1 explains 11% of the total sample variance and PC2 7.9%.

To determine the shape relationships between each of the samples, the scores of each operational taxonomic unit (OTU) on the resultant PCs are used as variables in a canonical discriminant analysis. In computing the discriminant function the inclusion of 'noisy' data that does not differentiate between the samples adds to dimensionality at the cost of discriminatory power (Viðarsdóttir and O'Higgins, 2003). This 'noise' may be due to higher PCs illustrating aspects of shape variation that are sample specific, such as sexual dimorphism and specific intra-population differences. To assess the effects of these 'noisy' factors, therefore, separate discriminant analyses with crossvalidation are undertaken using differing amounts of variance as follows: 70% (PC1-22), 80% (PC1-34), 90% (PC1-55), 95% (PC1-74) and 100% (PC1-138). Table 3.3 presents the results of the alternate discriminant analyses. The results reveal that the utilization of approximately 95% of the total variance gives optimal crossvalidation and thus discrimination between all samples and all further analyses in this chapter are thus undertaken using PCs1-74.

Figure 3.1. Indian Ocean rim: PC 1 v PC 2

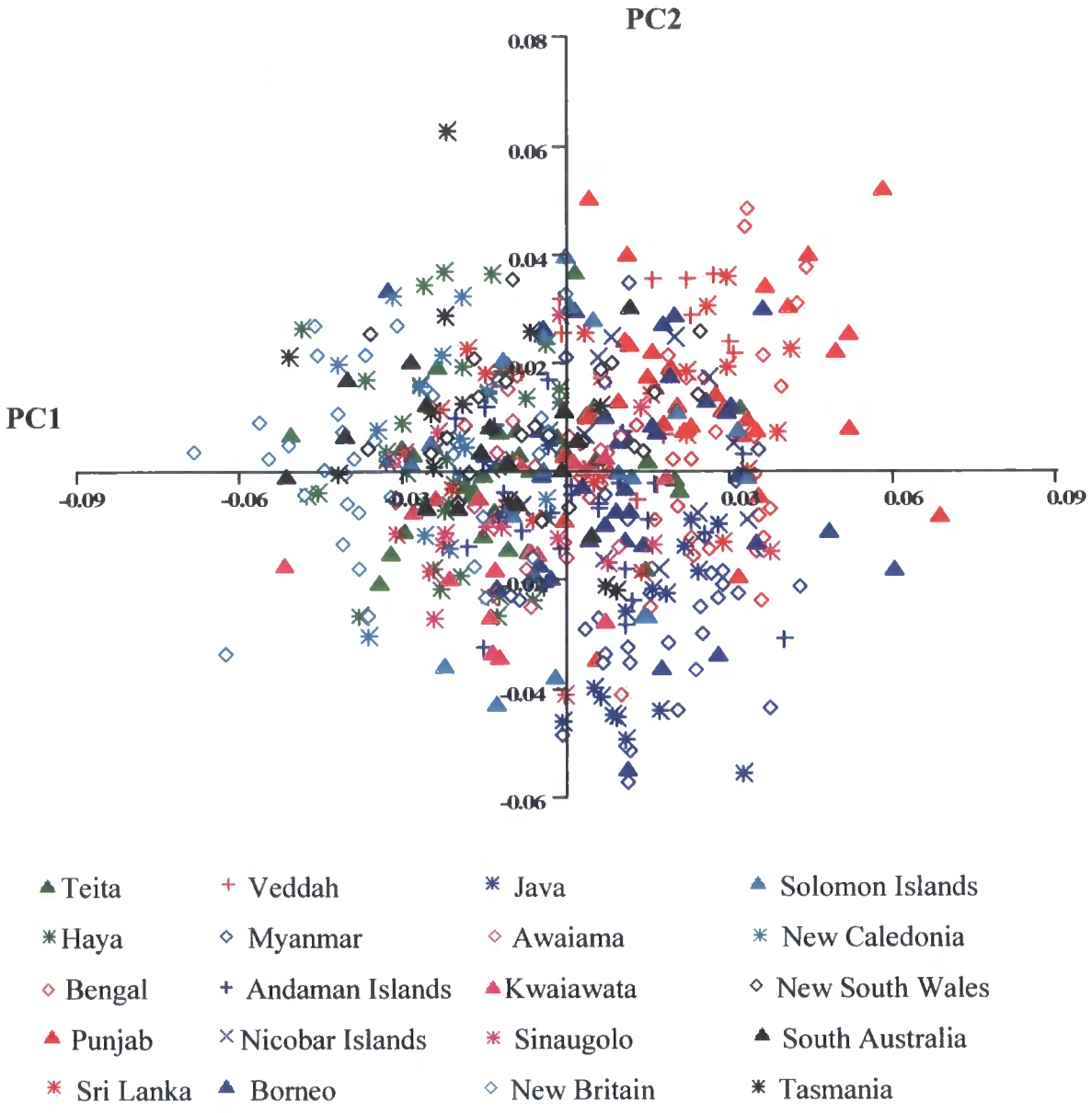


Table 3.2 Indian Ocean rim: The proportion of and accumulated variance of PCs 1 – 134, which account for 100% of total sample variance

PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %
1	11.00	11.00	**35**	0.65	80.60	**69**	0.23	93.90	**103**	0.08	98.60
2	7.86	18.90	**36**	0.61	81.20	**70**	0.22	94.10	**104**	0.08	98.70
3	6.49	25.30	**37**	0.60	81.80	**71**	0.22	94.30	**105**	0.08	98.80
4	4.91	30.20	**38**	0.58	82.40	**72**	0.21	94.50	**106**	0.07	98.90
5	4.82	35.10	**39**	0.57	82.90	**73**	0.20	94.70	**107**	0.07	98.90
6	3.76	38.80	**40**	0.54	83.50	**74**	0.19	94.90	**108**	0.07	99.00
7	3.14	42.00	**41**	0.54	84.00	**75**	0.19	95.10	**109**	0.07	99.10
8	2.92	44.90	**42**	0.52	84.50	**76**	0.18	95.30	**110**	0.06	99.10
9	2.76	47.60	**43**	0.51	85.00	**77**	0.18	95.50	**111**	0.06	99.20
10	2.65	50.30	**44**	0.48	85.50	**78**	0.17	95.60	**112**	0.06	99.20
11	2.34	52.60	**45**	0.47	86.00	**79**	0.17	95.80	**113**	0.06	99.30
12	2.29	54.90	**46**	0.46	86.50	**80**	0.17	96.00	**114**	0.05	99.30
13	1.94	56.90	**47**	0.45	86.90	**81**	0.16	96.10	**115**	0.05	99.40
14	1.83	58.70	**48**	0.42	87.30	**82**	0.16	96.30	**116**	0.05	99.40
15	1.69	60.40	**49**	0.41	87.70	**83**	0.15	96.40	**117**	0.05	99.50
16	1.56	61.90	**50**	0.40	88.10	**84**	0.15	96.60	**118**	0.04	99.50
17	1.45	63.40	**51**	0.39	88.50	**85**	0.14	96.70	**119**	0.04	99.60
18	1.44	64.80	**52**	0.37	88.90	**86**	0.14	96.90	**120**	0.04	99.60
19	1.41	66.20	**53**	0.37	89.30	**87**	0.13	97.00	**121**	0.04	99.70
20	1.31	67.60	**54**	0.36	89.60	**88**	0.13	97.10	**122**	0.04	99.70
21	1.24	68.80	**55**	0.34	90.00	**89**	0.13	97.30	**123**	0.03	99.70
22	1.18	70.00	**56**	0.33	90.30	**90**	0.12	97.40	**124**	0.03	99.80
23	1.14	71.10	**57**	0.32	90.60	**91**	0.12	97.50	**125**	0.03	99.80
24	0.96	72.10	**58**	0.31	90.90	**92**	0.11	97.60	**126**	0.03	99.80
25	0.95	73.00	**59**	0.31	91.20	**93**	0.11	97.70	**127**	0.03	99.80
26	0.87	73.90	**60**	0.30	91.50	**94**	0.10	97.80	**128**	0.03	99.90
27	0.87	74.80	**61**	0.29	91.80	**95**	0.10	97.90	**129**	0.02	99.90
28	0.83	75.60	**62**	0.29	92.10	**96**	0.10	98.00	**130**	0.02	99.90
29	0.79	76.40	**63**	0.28	92.40	**97**	0.10	98.10	**131**	0.02	99.90
30	0.76	77.10	**64**	0.27	92.70	**98**	0.09	98.20	**132**	0.02	100.00
31	0.74	77.90	**65**	0.26	92.90	**99**	0.09	98.30	**133**	0.02	100.00
32	0.71	78.60	**66**	0.25	93.20	**100**	0.09	98.40	**134**	0.02	100.00
33	0.68	79.30	**67**	0.24	93.40	**101**	0.09	98.50			
34	0.67	79.90	**68**	0.24	93.70	**102**	0.08	98.60			

Table 3.3 Cross validation study to assess the best separation by each proportion of sample variance

Sample	70% (PCs 1-22)	80% (PCs 1-34)	90% (PCs 1-55)	95% (PCs 1-74)	100% (PCs 1-138)
Teita	71.43	77.14	80.00	77.14	74.29
Haya	85.71	88.57	88.57	94.29	94.29
Bengal	31.43	40.00	34.29	42.86	45.71
Punjab	65.71	57.14	68.57	68.57	57.14
Sri Lanka	31.82	31.825	36.36	40.91	45.45
Veddah	66.67	53.33	46.67	46.67	20.00
Myanmar	68.57	82.86	88.57	74.29	77.14
Andaman Islands	73.53	79.41	88.24	94.12	88.24
Nicobar Islands	53.85	76.92	69.23	84.62	84.62
Borneo	42.86	48.57	51.43	48.57	57.14
Java	52.94	47.06	70.59	88.24	70.59
Awaiama	52.63	68.42	57.89	63.16	42.11
Kwaiawata	50.00	44.44	38.89	33.33	27.78
Sinaugolo	33.33	28.57	42.86	47.62	57.14
New Britain	68.57	82.86	82.86	82.86	74.29
Solomon Islands	28.57	23.81	28.57	33.33	42.86
New Caledonia	46.67	40.00	33.33	33.33	60.00
New South Wales	37.50	62.50	58.33	70.83	70.83
South Australia	68.75	68.75	62.50	56.25	56.25
Tasmania	33.33	50.00	41.67	50.00	50.00
Mean	**53.19**	**57.61**	**58.47**	**61.55**	**59.79**

The Mahalanobis' D distances between the samples are given in table 3.4. The largest Mahalanobis' distance is found between the Teita sample from Africa and the New South Wales sample from Australia. The smallest distance occurs between the Bengal and Punjab samples from India. All distances are statistically significant. A correlation between the variation between samples in PC1 revealed that 54% of this variation was found between the samples ($r^2 = 0.541$, $p < 0.001$).

Cross validation analysis is performed and the results are given in table 3.5. The percentage of correct classification for each individual sample ranges from 33.33% correct classification for the Kwaiawata, Solomon Island and New Caledonian samples, to 94.3% for the Haya sample. Approximately two thirds of all individual specimens are placed in their correct groups during cross validation. There is no significant correlation between the percentage of correct classification and number of individuals in each sample.

The samples with the lowest correct classification originated from the New Guinea and Melanesia regions; the Kwaiawata, New Caledonian and Solomon Island samples. Of these, the misidentified individuals from the Kwaiawata and New Caledonian samples are placed within the remaining Austro-Melanesian samples. The misidentified Solomon Island individuals, however, are spread more freely across all the samples, with the exception of the African samples. Similarly the samples from Sinaugolo and Borneo, both with less than 50% correct classification, also have misidentified individuals spread across the remaining samples. In contrast, the misidentified individuals from the Indian groups are generally placed within other Indian or South Asian samples.

Table 3.4 Mahalanobis' D distance matrix: Indian Ocean rim populations. All distances significant at $p < 0.001$ level

	Teita	Haya	Beng	Pun	SL	Ved	Mya	And	Nic	Bor	Java	Awai	Kwai	Sin	NB	SI	NC	NSW	SAus	Tas
Teita	0.00																			
Haya	28.65	0.00																		
Beng	39.85	34.34	0.00																	
Pun	51.54	43.56	9.10	0.00																
SL	42.98	37.18	9.14	14.77	0.00															
Ved	45.03	30.53	13.14	21.77	18.43	0.00														
Bur	42.89	40.49	25.93	35.71	29.36	36.49	0.00													
And	39.26	36.90	24.81	43.57	29.81	33.05	39.29	0.00												
Nic	59.88	59.11	43.04	48.28	52.17	45.26	44.10	50.48	0.00											
Bor	39.49	35.46	18.69	24.23	22.02	23.75	21.66	23.80	31.37	0.00										
Java	57.31	61.05	31.87	38.89	36.88	38.95	34.20	37.25	41.55	18.28	0.00									
Awai	52.18	51.44	38.32	44.13	32.82	39.79	50.37	40.83	49.10	24.26	32.90	0.00								
Kwai	49.52	45.06	33.73	38.05	31.31	37.45	40.51	38.42	41.83	17.04	23.97	24.44	0.00							
Sin	44.12	45.27	26.29	31.40	27.99	33.73	41.46	34.36	52.52	22.76	28.37	20.67	19.36	0.00						
NB	52.91	37.63	43.90	50.78	36.29	45.72	41.46	47.10	50.61	34.22	49.93	37.61	27.25	35.61	0.00					
SI	46.97	28.49	22.26	27.13	24.59	26.79	28.95	34.53	47.69	21.10	39.56	27.33	21.57	22.98	19.74	0.00				
NC	47.70	41.87	40.39	46.42	32.21	45.78	43.26	47.38	57.16	31.75	47.21	29.24	24.96	32.55	21.29	24.16	0.00			
NSW	64.36	46.01	32.71	34.97	29.29	28.94	46.56	50.43	55.45	33.10	43.33	32.93	28.97	30.75	29.47	19.44	34.99	0.00		
SAus	63.14	45.65	42.33	39.94	37.80	37.61	57.74	62.76	61.76	44.96	56.69	44.40	34.59	38.69	30.23	26.00	40.34	16.06	0.00	
Tas	62.21	49.92	40.06	41.11	39.60	45.90	56.61	48.27	55.18	35.97	52.24	38.47	33.56	32.59	35.06	24.93	43.74	28.33	26.92	0.00

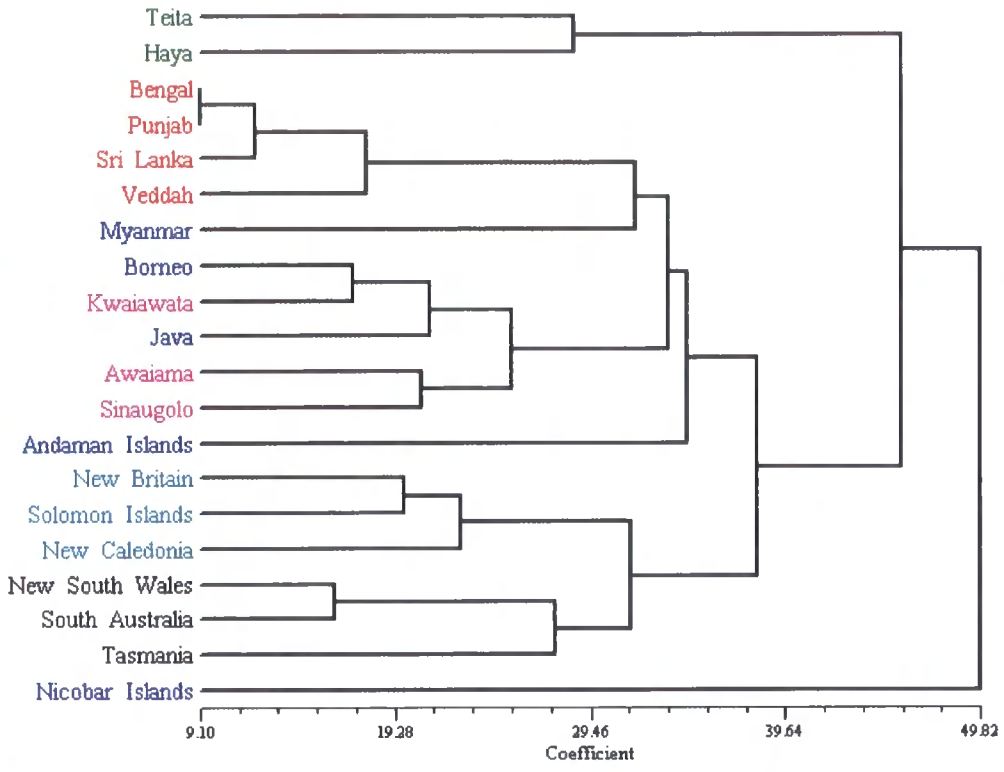
Table 3.5. Cross validation analysis: Indian Ocean rim populations

	Teita	Haya	Beng	Pun	SL	Ved	Mya	And	Nic	Bor	Java	Awai	Kwai	Sin	NB	SI	NC	NSW	SAus	Tas	Total
Teita	**77.14**	11.43	2.86	0.00	2.86	0.00	2.86	2.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
Haya	0.00	**94.29**	0.00	0.00	0.00	2.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.86	0.00	0.00	0.00	0.00	100.00
Beng	0.00	0.00	**42.86**	25.71	14.29	2.86	5.71	5.71	0.00	2.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
Pun	0.00	2.86	20.00	**68.57**	5.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.86	0.00	0.00	0.00	0.00	100.00
SL	0.00	9.09	22.73	13.64	**40.91**	9.09	0.00	0.00	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
Ved	0.00	0.00	26.67	13.33	6.67	**46.67**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	100.00
Mya	0.00	0.00	11.43	0.00	2.86	0.00	**74.29**	0.00	0.00	2.86	0.00	0.00	0.00	0.00	2.86	5.71	0.00	0.00	0.00	0.00	100.00
And	0.00	0.00	2.94	0.00	0.00	0.00	0.00	**94.12**	0.00	2.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
Nic	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**84.62**	7.69	0.00	0.00	0.00	0.00	7.69	0.00	0.00	0.00	0.00	0.00	100.00
Bor	0.00	2.86	0.00	0.00	2.86	2.86	2.86	2.86	0.00	**48.57**	11.43	0.00	11.43	8.57	0.00	2.86	0.00	2.86	0.00	0.00	100.00
Java	0.00	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	5.88	**88.24**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
Awai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.79	0.00	**63.16**	5.26	10.53	5.26	0.00	0.00	0.00	0.00	0.00	100.00
Kwai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.11	11.11	11.11	**33.33**	11.11	0.00	5.56	5.56	5.56	0.00	5.56	100.00
Sin	0.00	0.00	0.00	9.52	4.76	4.76	0.00	0.00	0.00	4.76	0.00	14.29	4.76	**47.62**	0.00	9.52	0.00	0.00	0.00	0.00	100.00
NB	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**82.86**	5.71	8.57	2.86	0.00	0.00	100.00
SI	0.00	0.00	0.00	4.76	0.00	0.00	14.29	0.00	0.00	0.00	0.00	0.00	4.76	0.00	9.52	**33.33**	4.76	19.05	0.00	9.52	100.00
NC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	13.33	0.00	20.00	26.67	**33.33**	0.00	0.00	0.00	100.00
NSW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.17	0.00	0.00	4.17	4.17	4.17	**70.83**	8.33	4.17	100.00
Saus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.25	6.25	0.00	0.00	31.25	**56.25**	0.00	100.00
Tas	0.00	0.00	0.00	8.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.33	0.00	8.33	8.33	0.00	16.67	**50.00**	100.00

The Mahalanobis' distances are used to generate a phenogram using UPGMA (figure 3.2). The distinct branches of the phenogram relate roughly to the regional groupings given to the populations (figure 3.2). The Nicobar Islands sample is seen to be a morphological outlier (figure 3.2), forming the first distinct branching in the phenogram. The cross validation results place 85% of the Nicobar individuals correctly within their group, showing that although placed as an outlier from the other samples, the Nicobar Islanders are morphologically homogeneous. The Nicobar Islanders are thus revealed as a very distinct group with little morphological similarity to the other samples under investigation.

Following the initial split of the Nicobar Islanders, the second obvious branching is between the African samples and the remainder of the Indian Ocean rim samples. Of the remaining samples, the samples from South Asia form a distinct branch. The Myanmar sample, however, clusters with the South Asian samples rather than the other Southeast Asian samples. A second bifurcaton is created by the samples from Southeast Asia and New Guinea. Within this cluster, the Kwaiawata group from New Guinea are positioned more closely to the Borneo and Java groups rather than with the other two samples from New Guinea. Finally a bifurcation from the South/Southeast Asian cluster is formed by the groups from Melanesia and Australia. Within this branch, the Melanesian groups form one cluster and the three Australian samples another. On this cluster of Australian samples, the Tasmanian sample is situated at a more distinct position than the samples from the mainland Australia.

Figure 3.2 Phenogram showing distances between the Indian Ocean rim samples, at a population level



3.4.2 Differences in craniofacial centroid size

The mean centroid size for each sample population is listed in table 3.6 and shown in figure 3.3. The mean centroid size is 400.37 with a standard deviation 16.81. The largest mean centroid size is represented by New Caledonia (413.77), though the largest individual specimen is from New Britain, with a centroid size of 438.12. The Andaman Island group have the smallest mean centroid size (374.11) and also the smallest individual specimen at 350.80. The mean centroid size of the Andaman Island group falls outside of the standard deviation for the total sample. All other mean centroid sizes fall within one standard deviation of the total sample mean.

Table 3.6 Indian Ocean rim: Mean facial centroid size

Population	Mean Centroid Size	Population	Mean Centroid Size
Andaman Islands	374.11	New Britain	404.76
Sri Lanka	388.15	New South Wales	405.69
Bengal	389.46	Solomon Islands	405.97
Veddah	390.27	Tasmania	406.00
Myanmar	396.49	Sinaugolo	407.10
Nicobar Islands	400.54	Haya	407.42
Punjab	401.53	Kwaiawata	407.53
Borneo	401.55	South Australia	408.96
Teita	404.15	Java	412.81
Awaiama	404.70	New Caledonia	413.77

To assess population specific differences in size an analysis of variance using the Hochberg *post hoc* test, is performed on the craniofacial centroid size and the results are listed in table 3.8. They reveal that differences in craniofacial centroid size are significant in 47 out of 190 comparisons. The individual principal components (table 3.2) are also correlated against centroid size. Table 3.7 presents the results of the correlation between centroid size and the first ten PCs of the complete sample. No significant correlation is found between any of the PCs and centroid size.

Figure 3.3 Indian Ocean rim: Mean facial centroid size

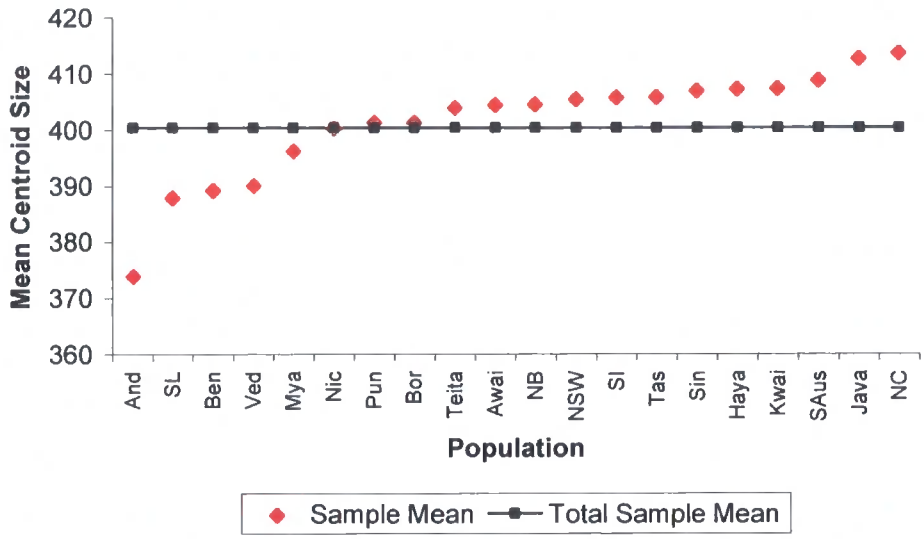


Table 3.7 Correlation between centroid size and PCs 1 to 10

	***r* value**	***p* value**
PC 1 v Centroid Size	0.24	0.310
PC 2 v Centroid Size	0.23	0.319
PC 3 v Centroid Size	0.27	0.241
PC 4 v Centroid Size	0.05	0.837
PC 5 v Centroid Size	0.11	0.654
PC 6 v Centroid Size	0.19	0.418
PC 7 v Centroid Size	0.17	0.480
PC 8 v Centroid Size	0.31	0.183
PC 9 v Centroid Size	0.07	0.775
PC 10 v Centroid Size	0.33	0.152

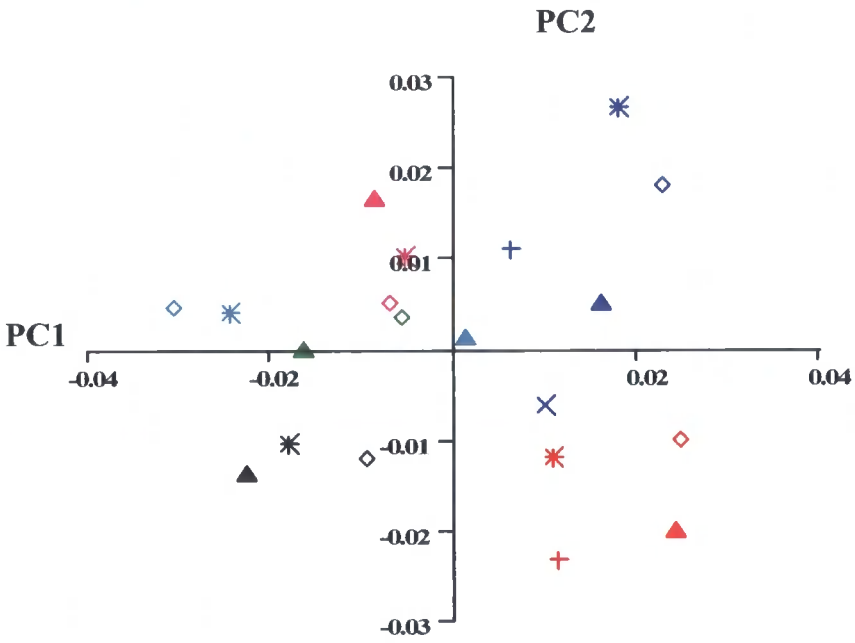
Table 3.8 ANOVA : centroid size

Teita	0.00																			
Haya	p=1.00	0.00																		
Ben	p<0.05	p<0.001	0.00																	
Pun	p=1.00	p=1.00	p=0.06	0.00																
SL	p<0.05	p<0.001	p=1.00	p=0.09	0.00															
Ved	p=0.23	p<0.05	p=1.00	p=0.82	p=1.00	0.00														
Mya	p=0.98	p=0.20	p=1.00	p=1.00	p=0.99	p=1.00	0.00													
And	p<0.001	p<0.001	p<0.05	p<0.001	p=0.05	p<0.05	p<0.001	0.00												
Nic	p=1.00	p=1.00	p=0.99	p=1.00	p=0.88	p=1.00	p=1.00	p<0.001	0.00											
Bor	p=1.00	p=1.00	p=0.06	p=1.00	p=0.09	p=0.81	p=1.00	p<0.001	p=1.00	0.00										
Java	p=0.99	p=1.00	p<0.001	p=0.70	p<0.001	p<0.05	p<0.05	p<0.001	p=0.96	p=0.71	0.00									
Awai	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p=0.42	p=1.00	p<0.001	p=1.00	p=1.00	p=1.00	0.00								
Kwai	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p=0.08	p=0.71	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	0.00							
Sin	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p=0.07	p=0.68	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	0.00						
NB	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p=0.15	p=0.92	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	0.00					
SI	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p=0.17	p=0.93	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	0.00				
NC	p=0.99	p=1.00	p<0.05	p=0.58	p<0.001	p<0.05	p<0.05	p<0.001	p=0.90	p=0.60	p=1.00	p=1.00	p=1.00	p=1.00	p=0.99	p=1.00	0.00			
NSW	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p=0.15	p=0.91	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	0.00		
SAus	p=1.00	p=1.00	p<0.05	p=1.00	p<0.05	p<0.05	p=0.46	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	0.00	
Tas	p=1.00	p=1.00	p=0.08	p=1.00	p=0.08	p=0.51	p=1.00	p<0.001	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	p=1.00	0.00
	Teita	Haya	Ben	Pun	SL	Ved	Mya	And	Nic	Bor	Java	Awai	Kwai	Sin	NB	SI	NC	NSW	Saus	Tas

3.4.3 Craniofacial shape variation between samples: Means

The analyses of the full dataset demonstrate that there are significant differences between the craniofacial shapes of the populations around the Indian Ocean rim. As no single PC separated the samples using the full dataset, sample means are examined to clarify the morphological relationships. The mean coordinates are obtained from a separate GPA of each sample and collectively subjected to a joint GPA and PCA. Figure 3.4 shows the results of the PCA for PC 1 versus PC2. The amount of variance accounted for by each of the PC is listed in table 3.9. PC1 accounts for 30% of the sample variance with PC 2 explaining a further 18% (table 3.9). No other single PC separates the sample populations. The Procrustes distances between the sample means are given in table 3.10. A strong and significant correlation is found between the Procrustes and Mahalanobis' distances from the full dataset ($r = 0.71$, $p < 0.001$).

Figure 3.4 Indian Ocean rim means: PC 1 v PC 2



▲ Teita	+ Veddah	✳ Java	▲ Solomon Islands
✳ Haya	◇ Myanmar	◇ Awaiama	✳ New Caledonia
◇ Bengal	+ Andaman Islands	▲ Kwaiawata	◇ New South Wales
▲ Punjab	× Nicobar Islands	✳ Sinaugolo	▲ South Australia
✳ Sri Lanka	▲ Borneo	◇ New Britain	✳ Tasmania

Table 3.9 Indian Ocean rim - means: The proportion and accumulated variance of PCs 1 – 19, which account for 100% of total sample variance

Principal Component	Variance %	Cumulative Variance %
1	30.0	30.0
2	17.6	47.6
3	8.8	56.4
4	7.4	63.8
5	6.4	70.2
6	5.1	75.3
7	4.7	80.0
8	3.4	83.4
9	3.2	86.6
10	2.5	89.1
11	2.1	91.2
12	2.0	93.2
13	1.6	94.8
14	1.5	96.3
15	1.1	97.4
16	1.1	98.5
17	0.7	99.2
18	0.5	99.7
19	0.3	100.0

Table 3.10 Procrustes distance matrix: Indian Ocean rim populations.

	Teita	Haya	Beng	Pun	SL	Ved	Mya	And	Nic	Bor	Java	Awai	Kwai	Sin	NB	SI	NC	NSW	SAus	Tas
Teita	0.0000																			
Haya	0.0349	0.0000																		
Beng	0.0450	0.0532	0.0000																	
Pun	0.0508	0.0563	0.0237	0.0000																
SL	0.0429	0.0453	0.0249	0.0288	0.0000															
Ved	0.0460	0.0497	0.0288	0.0365	0.0331	0.0000														
Mya	0.0484	0.0543	0.0378	0.0478	0.0433	0.0523	0.0000													
And	0.0418	0.0433	0.0394	0.0515	0.0382	0.0460	0.0419	0.0000												
Nic	0.0441	0.0498	0.0420	0.0425	0.0422	0.0413	0.0470	0.0462	0.0000											
Bor	0.0406	0.0461	0.0302	0.0359	0.0317	0.0386	0.0302	0.0346	0.0366	0.0000										
Java	0.0502	0.0593	0.0430	0.0536	0.0496	0.0567	0.0311	0.0429	0.0491	0.0359	0.0000									
Awai	0.0393	0.0447	0.0473	0.0512	0.0409	0.0485	0.0527	0.0430	0.0421	0.0418	0.0459	0.0000								
Kwai	0.0379	0.0403	0.0477	0.0532	0.0416	0.0516	0.0435	0.0381	0.0455	0.0355	0.0371	0.0330	0.0000							
Sin	0.0360	0.0449	0.0423	0.0492	0.0406	0.0479	0.0459	0.0393	0.0477	0.0399	0.0399	0.0307	0.0290	0.0000						
NB	0.0458	0.0391	0.0611	0.0660	0.0512	0.0562	0.0606	0.0491	0.0552	0.0526	0.0607	0.0461	0.0371	0.0412	0.0000					
SI	0.0375	0.0393	0.0322	0.0394	0.0325	0.0377	0.0376	0.0349	0.0415	0.0288	0.0405	0.0382	0.0305	0.0299	0.0393	0.0000				
NC	0.0437	0.0404	0.0567	0.0603	0.0456	0.0543	0.0588	0.0492	0.0552	0.0483	0.0579	0.0416	0.0351	0.0402	0.0296	0.0396	0.0000			
NSW	0.0435	0.0437	0.0413	0.0440	0.0342	0.0377	0.0520	0.0444	0.0443	0.0412	0.0519	0.0368	0.0376	0.0363	0.0393	0.0308	0.0380	0.0000		
SAus	0.0467	0.0467	0.0563	0.0567	0.0493	0.0500	0.0620	0.0570	0.0511	0.0555	0.0617	0.0466	0.0437	0.0451	0.0415	0.0425	0.0450	0.0307	0.0000	
Tas	0.0431	0.0385	0.0500	0.0521	0.0429	0.0448	0.0574	0.0472	0.0476	0.0449	0.0577	0.0414	0.0411	0.0399	0.0344	0.0351	0.0402	0.0315	0.0345	0.0000

Some clustering of the sample means by region is evident in figure 3.4, for example the three Australian samples are situated in the lower left hand quadrant of the graph. Some overlapping of the samples is, however, also apparent, particularly with the African, Melanesian and New Guinean samples. One noticeable cluster is the separation of the South and Southeast Asian samples placed on the positive end of PC1 from the remaining populations on the negative axis (figure 3.4). Figure 3.5 illustrates the mean configurations at the negative and positive extremes of PC1. At the negative extreme the shape is characterised by a relatively posteriorly sloping face (figure 3.5 i) with a relatively posteriorly and superiorly positioned glabella (figure 3.5 ii) and a prognathic maxilla (figure 3.5 iii). As the shape is warped to the positive extreme the maxilla becomes more relatively posteriorly positioned, tucked in beneath the upper face (figure 3.5 iv). Glabella is situated more superiorly towards the positive extreme of PC1 (figure 3.5 v) and the area between glabella and the bottom of the nasal cavity increases relatively in length (figure 3.5 vi). The cranial base is relatively longer at the negative than at the positive extreme of PC1 (figure 3.5 vii) and also the relative cranial height increases (figure 3.5 viii), with a superior displacement of landmark 15, defined as the point where the coronal suture intersects with the superior edge of the sphenoid.

The morphological changes along PC2 are illustrated in figure 3.6. PC2 separates the Australian samples from those of Africa, Melanesia and Papua New Guinea. There is also separation of the South Asian samples from the Southeast Asians, with the latter placed towards the positive extreme (figure 3.4). The shape at the negative extreme is characterised by a relatively flat face (figure 3.6 i) that becomes more posteriorly sloping towards the positive extreme (figure 3.6 ii). Associated with this difference are the relative position of glabella, which is placed more posteriorly and superiorly at the positive extreme (figure 3.6 iii) and the relative inferior displacement of the zygomatic (figure 3.6 iv). The posterior section of the cranium becomes more relatively anteriorly positioned along the positive axis of PC2 (figure 3.6 v).

Figure 3.5 Indian Ocean rim means. PC1 TPS: Differences in shape along the first PC. The upper figure represents the mean landmark configuration warped along PC1 from the negative to the positive extreme

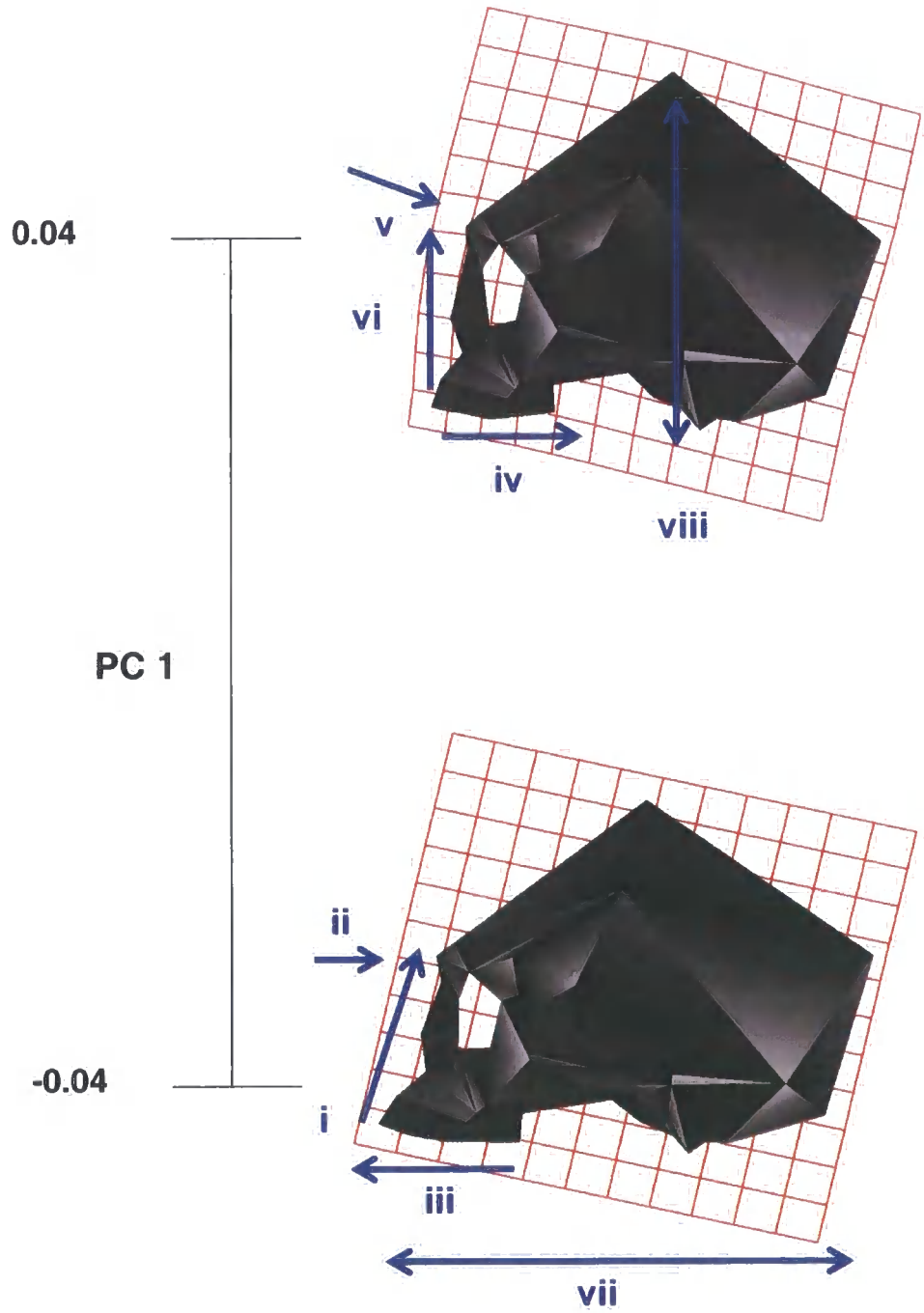
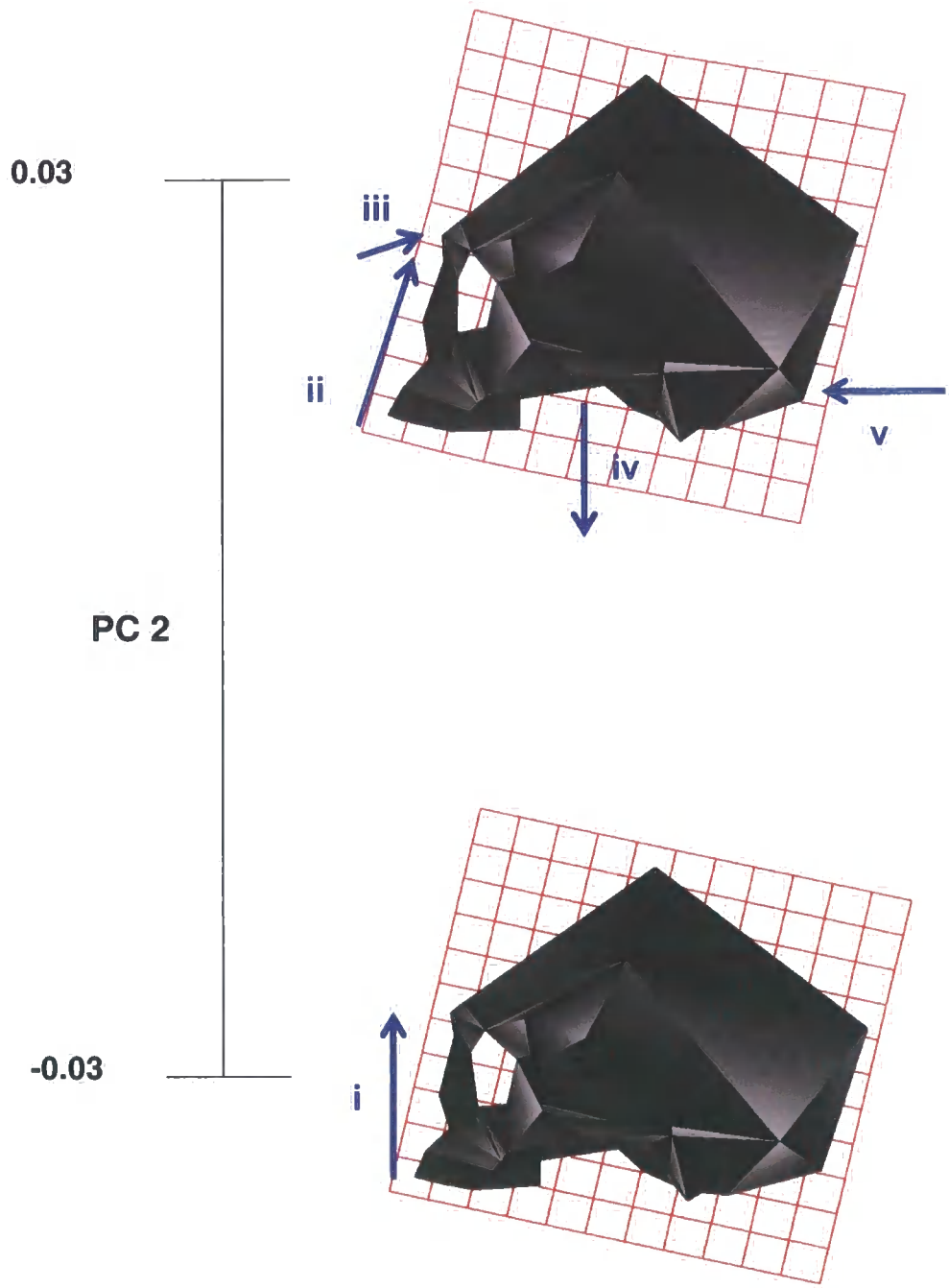


Figure 3.6 Indian Ocean rim means. PC2 TPS: Differences in shape along the second PC. The upper figure represents the mean landmark configuration warped along PC2 from the negative to the positive extreme



3.4.4 Craniofacial shape variation at the regional level

In both the analyses of the full dataset and the sample means a pattern of regional clustering of the populations is apparent. To test the strength of this pattern, a cross validation is performed on the regional clusters from South Asia, Southeast Asia, New Guinea, Melanesia and Australia. All regional groups are correctly classified at approximately 70% or over (table 3.11), with the African group achieving 92.86% correct placement, giving higher percentages than when using the individual samples. The greatest distinction of groups in the regional cross validation is found between Australia and Africa. No misclassified individuals from either group are placed in the other. Similarly the greatest Mahalanobis' distance at a regional level is found between the African and Australian group. The New Guinea and Melanesian groups are the least cohesive, with the smallest percentage of correct classification. The misidentified individuals from New Guinea are placed in all but the African groups. In the case of the Melanesian groups, misclassified individuals are placed in each of the other regions.

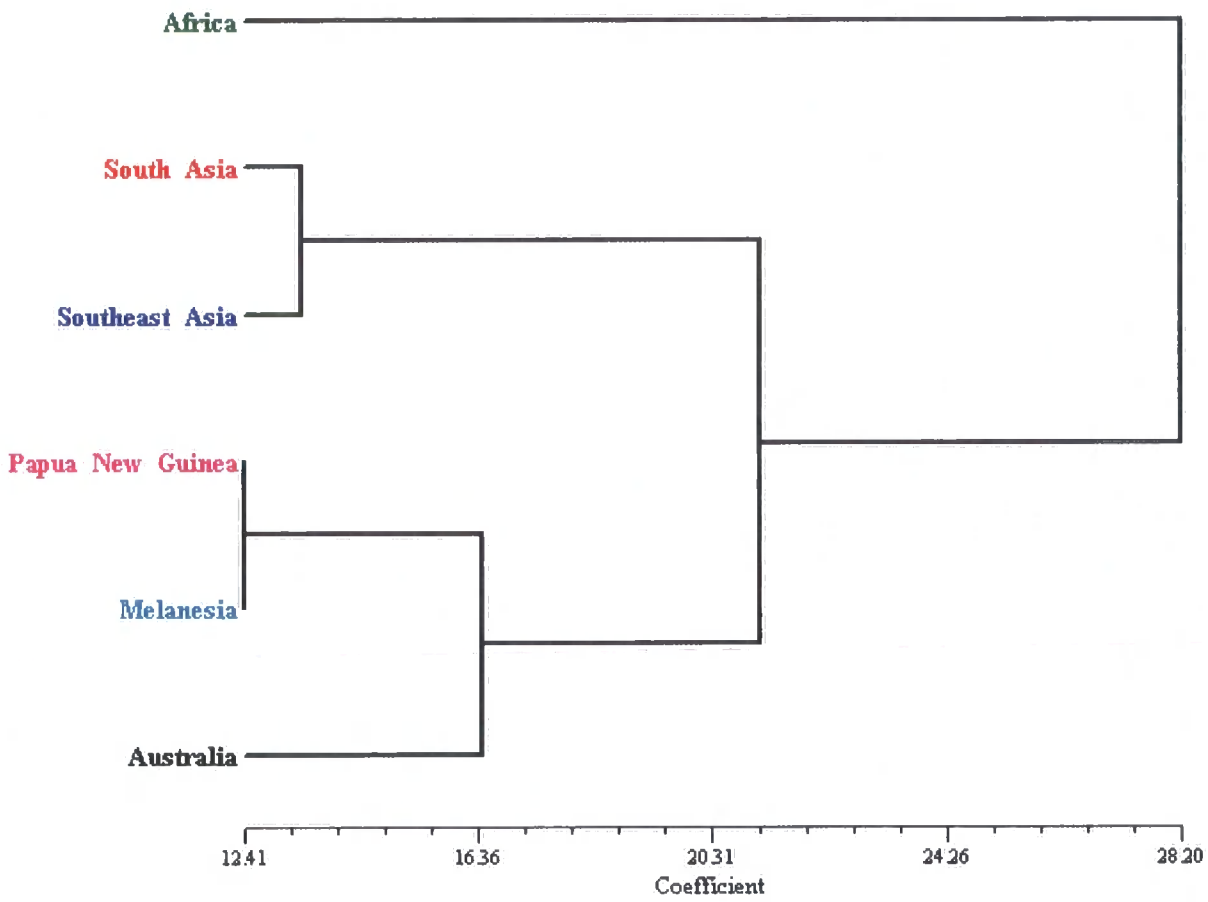
Table 3.11 Cross validation analysis: Indian Ocean rim - regions

	Africa	South Asia	Southeast Asia	New Guinea	Melanesia	Australia	Total
Africa	**92.86**	1.43	2.86	0.00	2.86	0.00	100.00
South Asia	2.80	**90.65**	4.67	0.00	0.93	0.93	100.00
Southeast Asia	1.49	8.96	**79.85**	5.22	4.48	0.00	100.00
New Guinea	0.00	1.72	10.34	**70.69**	12.09	5.17	100.00
Melanesia	1.41	1.41	5.63	11.27	**69.01**	11.27	100.00
Australia	0.00	3.85	0.00	7.69	11.54	**76.92**	100.00

A UPGMA phenogram is constructed based on Mahalanobis' distances between regional samples (see table 3.1 for regional information). The placement of the samples from New Guinea is contrasted in the individual sample and regional level phenograms (Figures 3.2 and 3.7). In the population level phenogram (figure 3.2), the New Guinea groups are to be found positioned with the Southeast Asian groups, as part of the larger South/Southeast Asian cluster. In the regional level phenogram (figure 3.7), New Guinea is positioned with Melanesia in a more general Australo-Melanesian cluster. It

is important to note whilst considering these results that while a phenogram is a useful tool for emphasising the morphological similarity of certain samples, or to stress distantly linked samples, this method does not allow sufficient recognition of samples positioned between major clusters (Matsumura and Hudson, 2005). When reducing a multidimensional relationship to a 2 dimensional phenogram, intermediately positioned samples such as the groups from the New Guinea area may occasionally aggregate with one or other of the major clusters in the phenogram.

Figure 3.7 Phenogram showing distances between the Indian Ocean rim samples at a regional level



3.4.5 Shape variation and geographic signals

3.4.5a Shape distance and geographic distance

To test whether there are any effects of geographic signals on craniofacial morphology two sets of analyses are undertaken. In the first analysis the Procrustes distances between the sample means, as calculated in Chapter 3, are correlated against geographic distances between the samples. Geographic distance is measured by two methods. A minimum distance between each of the populations is calculated using the distance between the latitude and longitude coordinates of the samples (table 3.12 and table 3.13). Where specific location of origin of the sample is unknown a central locale is taken for that sample. A weak but significant correlation is found between biological distance (as represented by the Procrustes distances) and minimum geographic distance ($r = 0.356$, $p < 0.0001$). Distances intended to emulate the possible coastal route taken during the proposed Late Pleistocene dispersal are also calculated. This second set of distances are estimated from measurements taken between samples using present day coastal pathways (table 3.14). A correlation between the coastal distances and the Procrustes distances found a similar significant result from these larger distances to that given by the minimum distances ($r = 0.307$; $p < 0.0001$).

3.4.5b Craniofacial shape and geographic distance

The second set of analyses to assess the effects of geographic signalling on craniofacial morphology correlates specific shape variance against latitude and longitude. In order to test for the effects of geographic signalling, the mean score of the first ten PCs of the complete dataset are correlated against the latitudinal and longitudinal coordinates of the populations, given in table 3.12. All latitudinal coordinates are counted as positive in order to account only for the effect of distance from the equator. Latitude is found to have a strong and significant negative correlation with PC3 ($r = -0.543$, $p = 0.013$). PC3 accounts for 8.8% of the total sample variance. Longitude is strongly and significantly correlated with both PC4, explaining 7.4% of the total variance ($r = 0.601$, $p = 0.005$), and PC9, explaining 3.2% of the total sample variance ($r = 0.608$, $p = 0.004$).

Table 3.12 Latitude and longitude coordinates for Indian Ocean rim samples

Region	Population	Latitude	Longitude
Africa			
	Teita	3.35	39.67
	Haya	1.33	31.81
South Asia			
	Bengal	22.63	88.42
	Punjab	31.52	74.40
	Sri Lanka	6.93	79.85
	Veddah	6.05	80.22
Southeast Asia			
	Myanmar	22.00	96.08
	Andaman Islands	11.67	92.75
	Nicobar Islands	9.17	92.78
	Borneo	1.42	110.33
	Java	6.17	106.83
Melanesia			
	Awaiama	10.23	150.53
	Kwaiawata	8.92	151.92
	Sinaugolo	9.46	147.19
	New Britain	4.20	152.18
	Solomon Islands	9.43	159.95
	New Caledonia	22.27	166.45
Australia			
	New South Wales	33.88	151.22
	South Australia	35.12	139.27
	Tasmania	42.92	147.33

Table 3.13 Minimum distances between samples calculated from longitude and latitude coordinates (km)

Teita	0																			
Haya	786	0																		
Ben	6,119	6,671	0																	
Pun	5,410	5,775	1,707	0																
SL	4,726	5,414	1,953	2,785	0															
Ved	4,745	5,442	2,025	2,891	107	0														
Mya	6,854	7,433	801	2,403	2,411	2,455	0													
And	6,225	6,893	1,292	2,902	1,513	1,515	1,193	0												
Nic	6,171	6,858	1,553	3,125	1,445	1,428	1,460	277	0											
Bor	8,004	8,747	3,326	5,032	3,435	3,381	2,737	2,240	2,121	0										
Java	7,575	8,347	3,762	5,417	3,329	3,251	3,327	2,515	2,606	938	0									
ANG	12,346	13,129	7,687	9,321	8,059	7,998	6,928	6,833	6,748	4,639	4,831	0								
KNG	12,517	13,300	7,753	9,369	8,185	8,125	6,985	6,931	6,855	4,756	4,982	212	0							
SNG	11,992	12,774	7,325	8,969	7,683	7,621	6,572	6,458	6,372	4,262	4,461	377	526	0						
NB	12,604	13,376	7,538	9,108	8,128	8,077	6,755	6,805	6,754	4,697	5,029	693	524	804	0					
SI	13,381	14,165	8,564	10,143	9,063	9,005	7,784	7,790	7,722	5,631	5,863	1,037	883	1,402	1,035	0				
NC	13,692	14,456	9,808	11,466	9,956	9,881	9,066	8,868	8,751	6,632	6,632	2,159	2,145	2,500	2,527	1,586	0			
NSW	11,870	12,606	9,129	10,834	8,751	9,659	8,506	7,976	7,794	5,804	5,502	2,622	2,767	2,738	3,291	2,854	1,966	0		
SA	10,769	11,510	8,345	10,027	7,793	7,671	7,767	7,129	6,923	5,056	4,617	2,985	3,176	2,954	3,676	3,539	2,997	1,107	0	
Tas	11,266	11,956	9,425	11,095	8,737	8,637	8,890	8,193	7,977	6,152	5,678	3,628	3,787	3,699	4,311	3,904	2,888	1,051	1,102	0
	Teita	**Haya**	**Ben**	**Pun**	**SL**	**Ved**	**Mya**	**And**	**Nic**	**Bor**	**Java**	**ANG**	**KNG**	**SNG**	**NB**	**SI**	**NC**	**NSW**	**SA**	**Tas**

Table 3.14 Distances between samples calculated from possible coastal routes (km)

Teita	0																			
Haya	1,000	0																		
Ben	15,263	16,263	0																	
Pun	10,407	11,407	6,944	0																
SL	12,710	13,710	2,553	4,391	0															
Ved	12,769	13,769	2,494	4,450	59	0														
Mya	16,348	17,348	1,085	8,029	3,638	3,579	0													
And	17,021	18,021	1,758	8,702	4,311	4,252	1,466	0												
Nic	17,618	18,618	2,355	9,299	4,908	4,849	2,063	597	0											
Bor	20,599	21,599	5,336	12,280	7,889	7,830	4,251	4,340	4,937	0										
Java	20,397	21,397	5,134	12,078	7,687	7,628	2,990	4,153	4,750	1,888	0									
Awai	25,602	26,602	10,339	17,283	12,892	12,833	8,195	9,358	9,955	7,093	5,205	0								
Kwai	25,822	26,822	10,559	17,503	13,112	13,053	8,415	9,578	10,175	7,313	5,425	220	0							
Sin	25,182	26,182	9,919	16,863	12,472	12,413	7,775	8,938	9,535	6,673	4,785	420	640	0						
NB	27,002	28,002	11,739	18,683	14,292	14,233	9,595	10,758	11,355	8,493	6,605	1,400	1,620	1,820	0					
SI	27,902	28,902	12,639	19,583	15,192	15,133	10,495	11,658	12,255	9,393	7,505	2,300	2,520	2,720	900	0				
NC	30,392	31,392	15,129	22,073	17,682	17,623	12,985	14,148	14,745	11,883	9,995	4,790	5,010	5,210	3,390	2,490	0			
NSW	27,933	28,933	12,670	19,614	15,223	15,164	10,526	11,689	12,286	11,169	7,536	4,370	4,590	3,950	5,770	6,670	9,160	0		
SAus	29,678	30,678	14,415	21,359	16,968	16,909	12,271	13,434	14,031	11,169	9,281	6,115	6,335	5,695	7,515	8,415	10,905	1,745	0	
Tas	29,044	30,044	13,781	20,725	16,334	16,275	11,637	12,800	13,397	10,535	8,647	5,481	5,701	5,061	6,881	7,781	10,271	1,111	1,306	0
	Teita	**Haya**	**Ben**	**Pun**	**SL**	**Ved**	**Mya**	**And**	**Nic**	**Bor**	**Java**	**Awai**	**Kwai**	**Sin**	**NB**	**SI**	**NC**	**NSW**	**SAus**	**Tas**

3.4.6 Shape variation and migration out of Africa

To specifically explore the effects of the southern dispersal on the samples from around the Indian Ocean rim, correlations between the geographical distances from Africa and shape distances from Africa are examined. The correlations are performed using both the direct and coastal distances from Africa, taken from tables 3.13 and 3.14. The geographical distance from Australia, one of the terminal points of the proposed dispersal, is also correlated as a test against the effects of isolation by distance. A significant correlation is found between geographic and shape distance from Africa in all but one case (table 3.15). The correlation between shape distance and the coastal distance using the Teita sample is only just non significant. The correlation using the two African populations combined provides a stronger correlation than that found when correlating all geographic and shape distances from around the Indian Ocean rim. A weak but statistically significant correlation is found between the minimum geographic distance from Australia and shape distance, the coastal distance is not, however, significant (table 3.15).

Table 3.15 Correlation of geographic distance with shape distance

Procrustes Distance:	Minimum Distance	Coastal Distance
from Africa, Teita and Haya combined	r = -0.553 p < 0.001	r = -0.525 p = 0.001
from Africa, Teita only	r = -0.508 p = 0.031	r = -0.426 p = 0.078
from Africa, Haya only	r = -0.690 p = 0.002	r = -0.682 p = 0.002
from Australia	r = 0.291 p = 0.038	r = 0.167 p = 0.242

3.5 Discussion

3.5.1 Craniofacial shape variation between groups

A large body of work exists demonstrating that there is considerable variation in the craniofacial skeleton of modern human populations (e.g. Howells, 1989; Hanihara, 1996). A common finding of these works is that populations from different geographic areas can be differentiated from one another on the basis of the craniofacial skeleton. The present study aims to elucidate whether traces of a proposed Late Pleistocene dispersal from Africa taking the 'southern route' can be found in modern human populations. The first hypothesis therefore addressed the question of whether there are differences in craniofacial shape between the geographically distinct populations from along and around the Indian Ocean rim. Principal components analysis of the full data set did not show any clear separation of the twenty population samples along any single PC. This result is not surprising as only a small percentage of variance is explained by each of the separate PCs (table 3.2). PC1, for example, only explained 11% of the total sample variance. Statistically significant Mahalanobis' distances, however, were found between all twenty sample populations and a mean of almost 62% of all individuals were correctly classified into their original population group. The results of the multivariate analyses demonstrate that there are differences in craniofacial shape of the populations located around the Indian Ocean rim. The first hypothesis is therefore refuted. Although the twenty populations are distinguishable on craniofacial shape alone, there is only a low level of variation between the samples, as demonstrated by the considerable overlap along PCs 1 and 2 (figure 3.1). This finding is in agreement with the observation by Relethford (1994) that the greatest amount of human craniofacial variation is between rather than among populations.

A significant difference in craniofacial size was found between some of the populations. The South Asian samples on the whole have smaller centroid sizes than the remaining populations. This finding refutes $\mathbf{H_2}$. No correlation is found between craniofacial shape and centroid size and thus $\mathbf{H_3}$ is also refuted. Craniofacial differences do not occur due to the effect of scale on shape. Although there are significant differences in size in the populations under analysis, it is not size that is dictating the overall patterns of craniofacial diversity found.

A notable result of these analyses is the substantive regional clustering of craniofacial morphology and the clinal nature of these clusters (table 3.4; figure 3.7). In the crossvalidation analysis of the full dataset, misidentified individuals are on the whole placed within groups from their own region rather than geographically further away (table 3.5). This is also the case for the regional crossvalidation analysis (table 3.11) with the exception of the Melanesian group where misidentified individuals are placed in all other groups. The Melanesian group appears to share morphological similarities with both the New Guinea and the Australian groups, reflecting their geographic placement between these two areas. Van Vark *et al.* (2003) questioned the validity of using morphological data to reconstruct ancestral/descendent relationships among populations separated by long intervals of time. The above results, however, reveal that there is a clinal nature of craniofacial morphological variation across regions. Population groups that are close in terms of geography cluster together within the phenogram generated from the individual biological distances (figure 3.2). Clusters are identified which fit general regional patterns. Similarly, in the regional phenogram (figure 3.7), clear and statistically distinct regional clustering of the samples is observed. A South Asian cluster is grouped with a Southeast Asian cluster. This is morphologically distinct from the Australian and Melanesian group. Of interest is the placement of the three New Guinean samples within the general Southeast Asian cluster rather than with the Melanesians. This suggests that there could have been migration and back migration between these areas following the initial coastal migration out of Africa, fitting with what is known of the history of these regions (see Chapter 5). The extremely high percentages of correct classification that are found in the regional discriminatory analysis (table 3.11) further extend the view that there is some association of morphological and geographic clusters.

Whilst the clinal nature of craniofacial morphology is evident from the populations around the Indian Ocean rim, the analyses also reveal the significant differences between the two African samples and the remaining samples. This is evident from the analysis of both the full dataset and the regional groups. In the crossvalidation the African samples achieve very high percentages of correct classification, 77.14% and

94.29% in the full dataset analysis and 92.86% in the regional analysis (tables 3.5 and 3.11). In the phenogram produced by the Mahalanobis' distances of the full dataset the African samples are placed as outliers from all other samples bar the Nicobar Islanders (figure 3.2). Again in the regional phenogram the African group is the first to bifurcate from the other groups (figure 3.7). This morphological distinctiveness of the African samples has also been found by other researchers (Relethford and Harpending, 1994; Hanihara *et al.*, 2003) and can be interpreted as agreeing with the Recent African Origin theory which predicts that the greatest difference of physical characteristics will be found between Sub-Saharan African populations and other geographical populations.

Many researchers have observed that, in terms of morphology, African and Australian populations tend to occupy the same multivariate space (Howells, 1973, 1989; Guglielmino-Matessi *et al.*, 1979; Hanihara, 1996; Relethford and Harpending, 1994). Hanihara (1996), for example, found that Australians show closer craniofacial similarities to African populations than to Melanesians. Explanations for this supposed relationship have included the similarity in environment in which the populations live (Gugleilmino-Matessi *et al.*, 1979) and retention of an ancestral morphology (Stringer, 1992). As described above, however, the African samples are morphologically distinct from all the rest of the populations (see figure 3.7). The Australian samples, on the other hand, cluster with the samples from Melanesia and New Guinea, not with those from Africa.

3.5.2 Shape variation and geography

The strong regional morphological clusters observed in this data suggest a relationship between craniofacial shape and geography. Similarities within regions may be partly created by gene flow between the local populations, along with some local adaptation (González-José, *et al.*, 2003). Although these regional patterns exist, significant differences are found overall between the twenty populations from around the Indian Ocean rim. Previous research on craniofacial diversity has concluded that a positive relationship exists between increasing geographic separation and phenotypic distance between groups (Konigsberg, 1990; Lalueza, 1996; Gonzàlez-José *et al.*, 2001). The present study has shown that a certain degree of geographic patterning exists within the

craniofacial shape of the studied populations from around the Indian Ocean rim. Estimates of both a minimum distance and a proposed coastal distance found weak but significant correlations between biological and geographic distance. Statistically significant correlations are also found between latitude and longitude and a number of the lower order principal components representing specific shape variance (PC 3, and PCs 4 and 9 respectively). The results suggest that geographic distance has a small but important influence on craniofacial shape, affecting specific areas as indicated by the relevant principal components.

The samples studied show that close geographic neighbours are more similar in craniofacial shape than samples more distant from them. The tendency for more variation to occur among regional populations than among local populations agrees with the findings of Relethford (2002), who stated that this tendency is a reflection of the isolation by distance model. Biological distance between the samples is in part determined by geographic distance and therefore hypothesis $\mathbf{H_4}$, which stated that relationships in craniofacial shape are not determined by geographic signalling is refuted.

3.5.3 Shape variation and distance from Africa

It has been demonstrated that the pattern of craniofacial diversity around the Indian Ocean rim is in part determined by geography and the effects of isolation by distance. These findings suggest that population dispersal will have played some role in the determination of patterns of craniofacial variation that are found today around the Indian Ocean rim. In order to address whether this patterning was further determined specifically by the dispersal out of Africa during the Late Pleistocene, and more specifically the coastal route taken around the Indian Ocean, a second set of analyses was undertaken. Molecular data provide support for an African origin of all modern human populations, in that the greatest amount of genetic diversity is found within African populations (Prugnolle *et al.*, 2005). Additionally, genetic distance from Africa is an excellent predictor for the diversity of human populations (Prugnolle *et al.*, 2005; Ramachandran *et al.*, 2005). Having shown that geographic distance alone is a predictor of craniofacial diversity, the present study assessed the effects of distance from Africa. Both measures of geographic distance, minimum and coastal, produced a strong and

significant correlation with distance from Africa and biological distance (table 3.15). These correlations were stronger than those found using distances between all samples. To assess whether this finding was an artefact, distance from Australia was also correlated against biological distance. Australia was chosen as it represents one of the terminal points of the Late Pleistocene migration. A significant correlation was found between biological distance and the minimum geographic distances, although the strength of the correlation was weaker than both the distance from Africa and the overall geographic distance (table 3.15). The correlation using the estimated coastal distances was not significant. These results suggest that geographic distance from Africa is a good predictor of morphological distance for the populations found around the Indian Ocean rim. The stronger correlation using the distance from Africa is consistent with a founder effect starting at a single origin and that the southern coastal route is at least one possible pathway for the dispersal from Africa. Hypothesis $\mathbf{H_5}$ stated that craniofacial diversity is not determined by distance from Africa and is therefore refuted.

Ramachandran *et al.* (2005) suggest that the geographic expansion event from Africa may have happened in many small steps, with each such migration involving a sampling from the previous subset of the original population. The robust regional morphological groupings identified in Chapter 3 may be in part the effects of these 'sample' migration events. As each migration happens, the population that remains behind will be subject to population-specific mutation and drift, creating a regional morphological type that differs from the founding population and also the 'sample' migratory population. Differences between the parent and offspring groups may also arise due to the varying environments to which they have been exposed (effects of environment on craniofacial morphology will be discussed further in Chapter 4). Thus the pattern of diversity elucidated in the present study not only reflects the effects of an initial dispersal event but rather the effects of a series of founder effects with a single origin.

3.5.4 Summary of craniofacial shape variation around the Indian Ocean rim

The results from Chapter 3 can be interpreted as populations sharing a single ancestral population, suggested by the small amount of variance across all populations, from which diversification has occurred. Traces of the Late Pleistocene dispersal from Africa

can be identified in the patterns of craniofacial variation found today in the populations around the Indian Ocean rim. The morphological clusters across the broad geographic regions reflect in part the effects of sample migrations during this initial dispersal. Additionally a general pattern of isolation by distance has allowed drift to accumulate variation within these regions. Selection in response to regional specific environments and cultures may also have enhanced the differences between regions and thus the following chapter will address the effects of environmental conditions on craniofacial shape.

- This study agrees with previous research that overall craniofacial diversity is restricted, probably due to a single founding population

- The present day human populations found around the Indian Ocean rim can be statistically distinguished from one another despite the overall restriction of craniofacial diversity

- Craniofacial size is not correlated with shape

- Geography plays an important role in determining the patterns of craniofacial diversity found around the Indian Ocean rim. In part this is due to isolation by distance, however traces of the initial expansion of modern humans out of Africa is detectable in the craniofacial shape of the studied populations

- Strong regional clusters can be found within the overall pattern of diversity, possibly reflecting sample migratory populations from the initial dispersal event, serial founder effect and genetic drift. Adaptation to specific regional environments has not been tested in this chapter.

Chapter 4

Epigenetic effects on Craniofacial Shape

4.1 Introduction

Chapter 3 identified the patterns of craniofacial variation found on and around the Indian Ocean rim and addressed the role of dispersal and population movements on modern human variation. The present chapter will explore the effects of environmental and climatic factors which may have acted on the documented phenotypic variation found around the Indian Ocean rim. Previous research has identified convergent adaptation to the local environment as being one of the factors that go toward explaining craniofacial patterns among modern human populations (González-José *et al.*, 2003). The effects, if any, of climatic variables such as temperature and rainfall will be discussed below.

4.1.1 Shape variation and environmental adaptation

In addition to population dispersal, diversification of craniofacial morphology can also occur due to a variety of evolutionary mechanisms relating to the genetic effects of selective pressures from specific environmental conditions. The present differences in craniofacial morphology found between populations around the Indian Ocean rim may therefore be determined in part by local adaptation and microevolutionary forces. Previous research has shown that extreme physical environmental factors such as climate and altitude account for a variable proportion of the phenotypic diversity in craniofacial morphology. Howells (1973), for example, suggested that climate was a contributing factor in shaping the separation he found between Africans and Australians on one hand, and Europeans, Asians and Americans on the other.

The effects of extreme cold temperatures on craniofacial shape have been well documented in past research. Guglielmino-Matessi *et al.* (1979) examined the influence of temperature, relative humidity and precipitation and found cold stress to be a major climatic factor influencing cranial skeletal measurements. The distinct morphological

characteristics of Fuegians have been attributed to a combination of biomechanical and climatic adaptations (Hernández *et al.*, 1997). The study states that it is reasonable to expect the development of adaptations to a cold environment under the climatic circumstances of Tierra del Fuego and also the long-standing isolation of the population. In particular, the nasal morphology of the Fuegians is considered to have responded to the adaptive pressures of the cold climatic conditions (Hernández *et al.*, 1997). In a test of the neutral hypothesis of cranial evolution in living and recent humans, Roseman (2004) found a correlation between certain aspects of cranial facial shape and a measure of coldness of climate. Removing the effects of shared population history and structure did not alter this correlation. Roseman concluded that the action of natural selection, associated with regional variation in temperature, led to among-population differentiation in excess of neutral expectations for certain cranial dimensions. As with the Fuegians, this differentiation featured the nasal morphology and was associated with extreme cold temperatures (Roseman, 2004).

Local adaptation has also been postulated as a factor in shaping craniofacial morphology (González-José *et al.*, 2005). Mechanical loading of the skull, in particular relating to the masticatory apparatus, has been widely studied (Lahr and Wright, 1996; Giesen *et al.*, 2003). It has been suggested that by reducing masticatory muscle activity and thus reducing the mechanical loading of the craniofacial skeleton there is a decrease in muscle size and related skeletal structures (González-José *et al.*, 2005). One possible cause of these changes is the shift in subsistence behaviour from hunting and gathering to agriculture and food production, with a concomitant move to the consumption of softer foodstuffs. Experimental studies have shown that changing the consistency of the diet can contribute to modifications of cortical bone thickness and mandibular density (Bresin *et al.*, 1999) and changes to the maxilla, mandible and palate structures (Giesen *et al.*, 2003). Overall these studies suggest that differing levels of masticatory activity and stress can have a plastic effect on certain craniofacial skeletal structures, mainly located in the masticatory and alveolar regions. The background data available regarding the samples contained in this study unfortunately do not allow for an analysis of the subsistence behaviour of the populations under consideration. It must, however,

be considered that subsistence strategy may play a part in forming the patterns of craniofacial diversity found between the populations.

Hypotheses

It has been demonstrated that the human craniofacial skeleton is plastic and susceptible to changes in shape due to epigenetic forces. Mechanical stressors may play a part in determining the shape of the craniofacial skeleton, though this cannot be explored by the present data. Adaptations to environmental conditions have additionally been found to have a role in the formation of human craniofacial skeletal shape, in particular in response to extreme cold conditions. The present chapter will thus assess the degree to which environmental factors determine the patterns of craniofacial diversity found in the samples from on and around the Indian Ocean rim. As discussed above, previous studies of environment have found a relationship between cold temperatures and changes in craniofacial morphology. It is anticipated that as the populations included in this study are from mainly tropical regions, no association between climate and craniofacial shape will be found. The following null hypotheses are therefore erected:

H_1 "Relationships in craniofacial shape are not determined by current environmental variables"

H_2 "Relationships in craniofacial size are not determined by current environmental variables"

The climatic data tested are mean annual high and low temperatures and total annual precipitation. Indices of seasonality and productivity are also tested. The environmental variables are correlated against both biological distances and principal components. Hypothesis 1 is falsified if any of the environmental factors tested correlate significantly with the principal components and/or biological distances. Hypothesis 2 will be falsified if any of the environmental factors tested correlate significantly with size.

4.2 Materials

The skeletal samples analysed in Chapter 3 are used in these analyses.

4.3 Methods

The principal components calculated in Chapter 3 (table 3.2) are included in these analyses.

Geographic measures of distance

Minimum geographic distances and proposed coastal distances are applied as given in Chapter 3.

Biological distances

As only one data point for each environmental variable is available, biological distances are assessed using the Procrustes distances calculated between the mean groups as given in Chapter 3.

Climate variables

To estimate to what extent climatic factors determine geographic variation of craniofacial shape, the following variables are used: annual mean high temperature; mean annual low temperature and total annual precipitation. Climatic data is derived from the Weatherbase database, located on www.weatherbase.com and accessed on 22/08/05. The environmental variables, listed in table 4.1, are calculated at a single locale for each of the populations. For samples where the provenance is known data is taken from the nearest weather station. Where specific location of the provenance of the skeletal samples is not known, a central locale is chosen to obtain the environmental data.

Climate indices

In addition to the standard variables listed above, correlations between the principal components and two environmental indices are assessed, the Shannon index and the Primary Productivity Index (PPI), which measures the length of the plant growing

season. The Shannon index ranges from 0 (highly seasonal) to 1 (no seasonality). PPI equals the number of months per year receiving more rainfall (in millimetres) than twice the mean annual temperature for that site (in °Celsius).

Correlations

Correlation analysis is undertaken using Pearson's correlation coefficient (r) and associated p-value. Values are calculated using the statistical software package SPSS (SPSS for Windows, Rel. 14.0.2. 2006. Chicago: SPSS Inc.).

4.4 Results

4.4.1 Shape variation and environmental variables

The relationship between craniofacial shape and environmental factors is explored by two methods. Initially the environmental variables are examined for any correlation with the means of the first ten principal components. The first ten principal components are chosen as they account for approximately 50% of the total sample variance. The variables tested are average annual high and low temperature and average annual precipitation and are given in table 4.1. Correlations between shape and the biodiversity indices, the Shannon Index and the Primary Productivity Index (PPI) (table 4.1), are also examined.

PC1, which explains 11.0% of the total sample variance, correlates significantly with average high temperature, ($r = 0.450$, $p = 0.046$). A low score on this component indicates a relatively posteriorly sloping face (figure 4.1 i), with extreme maxillary prognathism (figure 4.1 ii). The shape at the negative extreme of PC1 is also characterised by a relatively longer basicranium (figure 4.1 iii). A high score on PC1 indicates a more relatively flattened face (figure 4.1 iv), with the maxilla positioned relatively more anteriorly beneath the nasal cavity and a relatively more prognathic nasal region (figure 4.1 v). In addition, with a move from the negative to positive extremes on PC1 there is an associated relative anterior and superior movement of glabella (figure 4.1 vi) and the basicranium becomes relatively more constricted (figure 4.1 vii). Associated with these changes, the position of bregma becomes more relatively posteriorly and superiorly positioned (figure 4.1 viii).

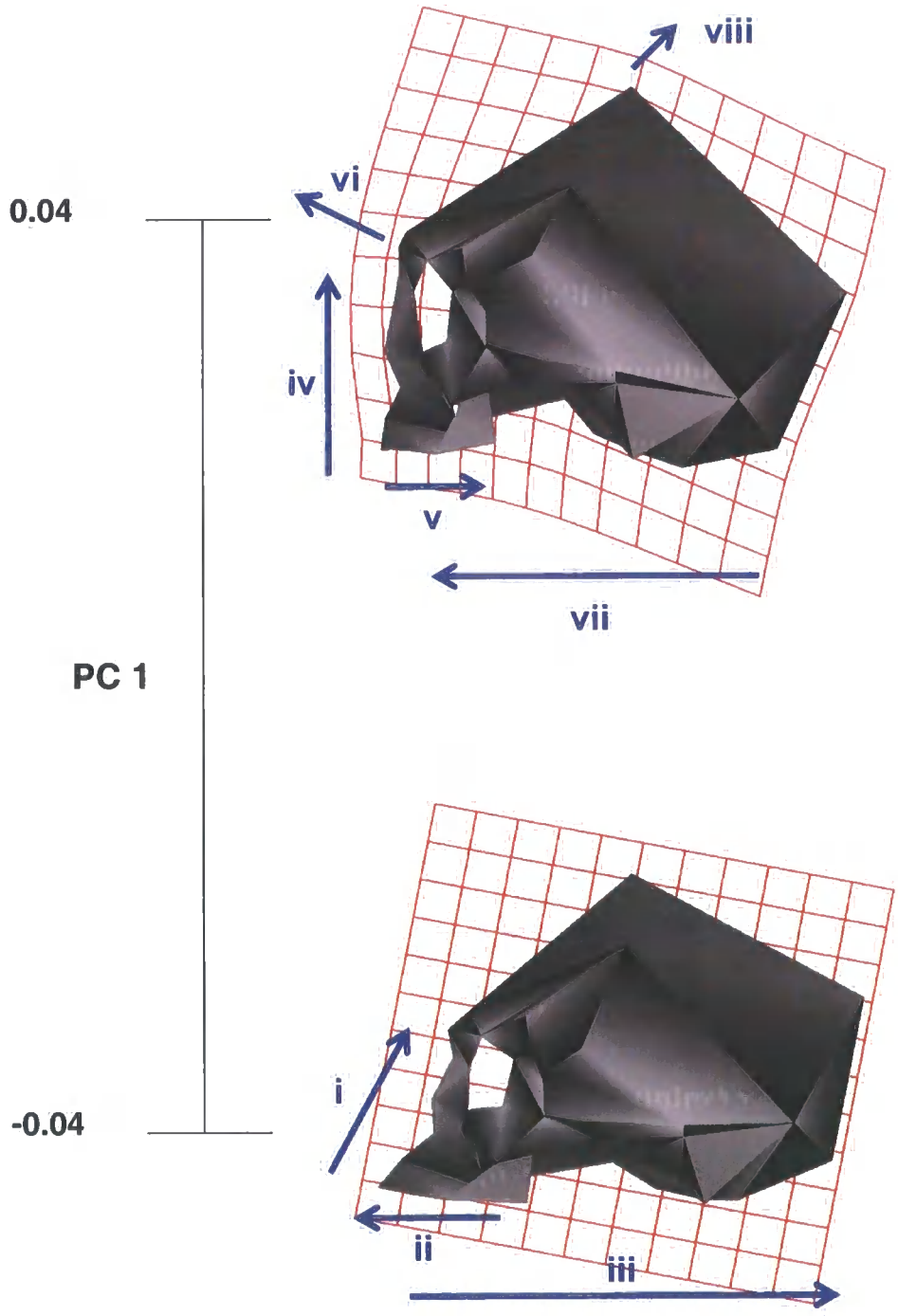
Table 4.1 Environmental variables for samples from the Indian Ocean rim

	Avg High Temp	Avg Low Temp	Total Annual Precipitation	SI	PPI
Teita	30	19	54	0.87	9
Haya	25	16	204	0.96	12
Bengal	30	22	152	0.80	6
Punjab	28	20	51	0.98	12
Sri Lanka	30	25	223	0.82	7
Veddah	30	25	240	0.94	11
Myanmar	32	21	87	0.93	12
Andaman Islands	28	25	293	0.99	12
Nicobar Islands	30	25	250	0.97	12
Borneo	31	23	388	0.98	9
Java	30	23	119	0.98	12
Awaiama	30	23	149	0.93	10
Kwaiawata	28	23	226	0.76	3
Sinaugolo	31	22	117	0.89	0
New Britain	31	23	202	0.95	12
Solomon Islands	30	22	217	0.98	8
New Caledonia	25	20	111	0.94	12
New South Wales	22	12	113	0.99	1
South Australia	22.5	9.8	34	0.79	4
Tasmania	16	8	60	0.97	12

Table 4.2 Correlations between PCs 1-10 and environmental variables

	Avg High Temp	Avg Low Temp	Total Annual Precipitation	SI	PPI
PC1	r = 0.450 p = 0.046	n/s	n/s	n/s	n/s
PC2	n/s	n/s	n/s	n/s	n/s
PC3	r = 0.474 p = 0.035	r = 0.549 p = 0.012	r = 0.553 p = 0.011	n/s	n/s
PC4	n/s	n/s	n/s	n/s	n/s
PC5	n/s	n/s	n/s	n/s	n/s
PC6	n/s	n/s	n/s	n/s	n/s
PC7	n/s	n/s	n/s	n/s	n/s
PC8	n/s	n/s	r = -0.559 p = 0.010	n/s	r = -0.674 p = 0.001
PC9	n/s	n/s	n/s	n/s	n/s
PC10	n/s	n/s	n/s	n/s	n/s

Figure 4.1 Indian Ocean rim. PC1 TPS: Differences in shape along the first PC. The upper figure represents the mean landmark configuration warped along PC1 from the negative to the positive extreme



PC3, which explains approximately 6.5% of the total sample variance, correlates significantly with average high temperature ($r = 0.474$, $p = 0.035$), average low temperature ($r = 0.549$, $p = 0.012$) and total annual precipitation ($r = 0.553$, $p = 0.011$). The most notable differences between the shape at the negative and positive extremes of PC3 are seen within the calvarium (figure 4.2). Warping from the negative to the positive extreme of PC3, lambda becomes relatively more superiorly and anteriorly positioned (figure 4.2 i), whilst inion is situated relatively more inferiorly and anteriorly (figure 4.2 ii). Stephanion is also placed relatively more inferiorly and anteriorly at the positive extreme (figure 4.2 iii). At the positive extreme of PC3 glabella is positioned more posteriorly (figure 4.2 iv).

PC8, explaining 2.9% of the sample variance, is strongly correlated with total annual rainfall ($r = -0.559$, $p = 0.01$). A strong and significant correlation is also found between PC8 and the primary productivity index (PPI) ($r = -0.674$, $p = 0.001$). The Shannon index has no significant correlation with any of the PCs. A low score on PC8 indicates a relatively prognathic maxilla (figure 4.3 i), which warps to a relatively more constricted position towards the positive extreme (figure 4.3 ii). Warping from the negative to the positive extreme also results in a relative anterior and superior positioning of the area above the nasal aperture (figure 4.3 iii), with glabella moving to a relatively more anterior position (figure 4.3 iv). Associated with these changes is a relatively inferior displacement of the position of bregma (figure 4.3 v), resulting in a decrease in cranial height towards the positive extreme of PC8 and a more anterior placement of lambda (figure 4.3 vi).

Figure 4.2 Indian Ocean rim. PC3 TPS: Differences in shape along the third PC. The upper figure represents the mean landmark configuration warped along PC3 from the negative to the positive extreme

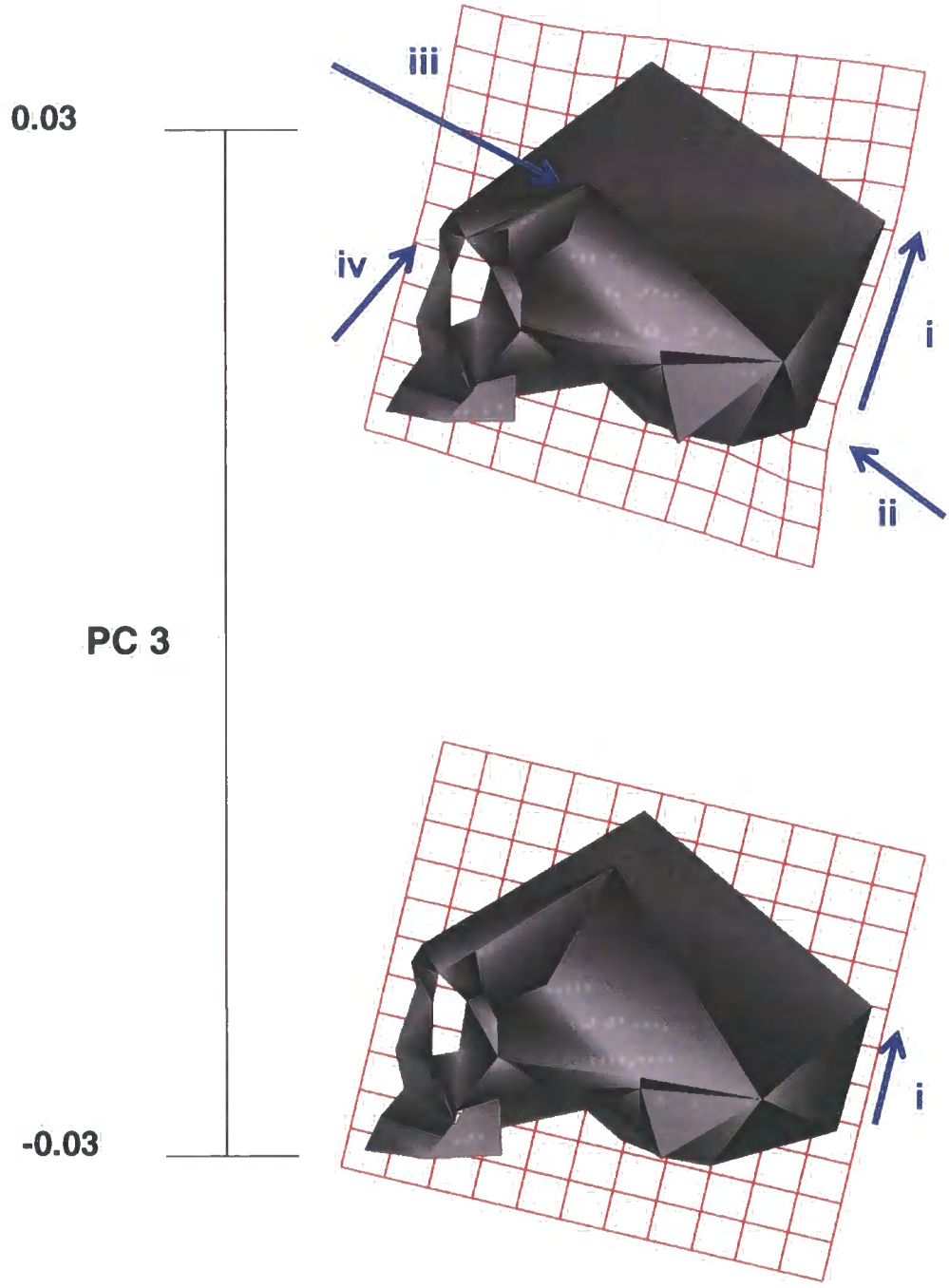
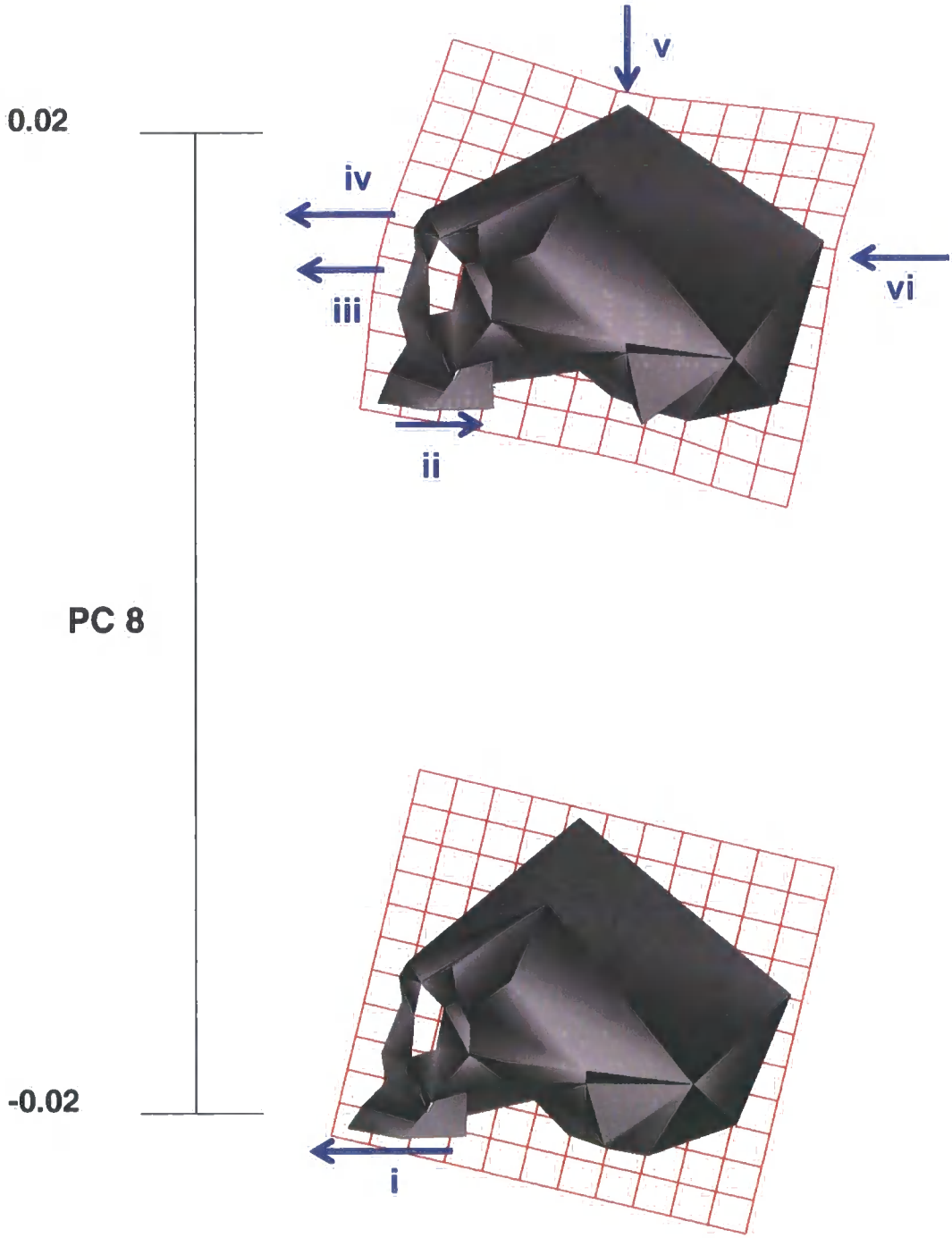


Figure 4.3 Indian Ocean rim. PC8 TPS: Differences in shape along the eighth PC. The upper figure represents the mean landmark configuration warped along PC8 from the negative to the positive extreme



4.4.2 Shape distance and the environment

A second set of analyses were undertaken to assess any possible effects of the environment on craniofacial shape. The Procrustes distances between each of the twenty samples are examined for correlations with the differences between the environmental variables (table 4.1). Weak but significant correlations were found between the Procrustes distances and average high temperature ($r = 0.153$, $p = 0.035$) and average low temperature ($r = 0.179$, $p < 0.014$) differences. No significant correlation was found with annual precipitation ($r = -0.047$, $p = 0.522$).

4.4.3 Shape variation and size

The mean centroid size for each sample population is correlated against latitude, longitude and the environmental variables (tables 3.12 and 4.1). No significant correlation is found between centroid size and any of the listed variables.

4.5 Discussion

4.5.1 Shape variation and environmental variables

The role of the environment, specifically in local adaptation to climatic variables, has been widely discussed in relation to human craniofacial morphology (Guglielmino-Matessi *et al.*, 1979; Hernández *et al.*, 1997; Roseman, 2004). Previous studies have found the levels of cranial diversity to be similar to those found genetically (Relethford, 1994; Relethford and Harpending, 1994), implying that regionally distinct selection pressures have played a limited role in producing contemporary morphological and genetic differentiation. The possibility exists, however, that some aspects of cranial variation have been subject to local environmental adaptation in the past, but that the effects of this were not pronounced enough to dominate a pooled analysis of cranial diversity (Roseman and Weaver, 2004). In the samples studied here, weak but significant correlations are found between average high and low temperature differences and the Procrustes distances between the populations. At this level of analysis no correlation is found between overall craniofacial shape and annual precipitation. Average high temperature also has a relatively strong and significant correlation with the first principal component. Principal component 3, which is characterised on the whole by differences in the calvarium region, correlates with both average high and low temperatures and most significantly with annual precipitation.

The weak but significant correlations between the temperature differences and the Procrustes distances show that temperature does have some influence on craniofacial shape. This result is interesting because in previous research only extreme cold temperatures have shown any correlation with craniofacial shape, although these studies have been undertaken using traditional craniometrics (Guglielmino-Matessi, 1979; Roseman, 2004). The correlation with biological distance reflects the overall craniofacial morphology rather than specific areas such as the change in nasal aperture shape in Roseman's study (2004). The use of traditional craniometric measurements may therefore not have perceived these relationships due to their two dimensional nature. Specific shape variation is also correlated with temperature and precipitation and the results of the multiple regression analyses suggest that a general relationship exists

between the morphology described by PC3 and levels of average temperature and precipitation. Precipitation levels usually reflect the influence of seasonality and prime productivity, although the seasonality indices did not produce significant correlations with PC3. In the previous chapter PC3 was found to correlate with latitude. Latitude itself has a significant correlation with temperature and precipitation. It appears therefore that the shape changes described along PC3 are the result of the gradient of latitude covered by the twenty samples. Interestingly PC8 achieves a strong and significant correlation with total annual precipitation and also with PPI. Although only explaining a small percentage of total variance, the shape changes along this PC do appear to be dictated by the amount of precipitation in the year. Since PPI is a measure of the length of the plant growing season it is possible to suggest that this variation is in some way related to food production and subsistence strategy. A number of studies on animals have related diet to modifications in the cranium and mandible (Giesen *et al.*, 2003; Ciochon *et al.*, 1997; Herring and Teng, 2000). It is likely, therefore, that the changes observed along PC8, associated with the cranial vault, the maxilla and the upper face (figure 4.3), are in some part the result of modifications due to subsistence strategy.

The effects of subsistence strategy and the plastic nature of the craniofacial skeleton is addressed by González-José *et al.* (2005) on a study of South American populations. The study revealed that a proportion of the variation in the morphology of the masticatory component of the South American craniofacial complex was driven by either a selective process or by plastic responses during ontogeny. It was also found, however, that differentiation at the craniofacial level remained stronger among populations than among groups that shared similar subsistence strategies. González-José *et al.* (2005) proposed that the levels of differentiation were more consistent with a scenario in which craniofacial divergence arose mainly as a result of disruption in the history and structure of the populations, rather than as a consequence of adaptation to particular selective pressures. As in the case of the populations studied in this chapter, environmental conditions play a small role in defining craniofacial morphology, although it appears that overall population history is a greater determinant of large scale diversity. The results of the current chapter agree with González-José *et al.* (2005) in

that, although plastic changes can generate changes in craniofacial morphology they are not fixed in the population genetic pool and are therefore unlikely to be long term causes of diversity.

The correlations with particular environmental conditions demonstrate an overall plasticity of the craniofacial skeleton and the effects of differing conditions on the development of the observed morphology. The potential existence of environmental forces acting upon the development of craniofacial shape may not, however, be sufficient enough to state that these conditions played an important role in the origin of overall morphological differences (Lahr and Wright, 1996; Relethford, 2002; González-José *et al.*, 2004). Although the craniofacial skeleton is demonstrably plastic in nature, the results of Chapter 3 demonstrate that geography and demographic history may be stronger in determining the overall pattern of diversity found around the Indian Ocean rim.

Climate may not only affect morphological diversity by acting on the more plastic regions of the craniofacial skeleton. Morphological diversity could also be created by the effects of climate on the movements of people over time and space, by limiting the mobility of populations and causing dispersal differentiation (Sardi *et al.*, 2005). It was proposed by Dillehay (1999), for example, that as the environment dried and cooled during the Pleistocene-Holocene transition, the mobility of the settlers of America was limited and they subsequently became more differentiated. If Late Pleistocene human populations were small, isolated and thus susceptible to population extinctions as may have been the case if the proposed 'sample' migrations occurred, then this could in part explain the extremes of variation found in the craniofacial skeleton of extant groups around the Indian Ocean rim. Eller *et al.* (2004) suggest that the Pleistocene populations occupied a large geographic range, with heterogenic environmental conditions and thus variable extinction rates would act on the dispersed populations. A model of population extinction and recolonisation is proposed as an alternative explanation for the Late Pleistocene population expansion suggested by the genetic data (Rogers and Harpending, 1992). Such local extinctions could also have the effect of reducing craniofacial skeletal

diversity, which, along with the effects of drift, could have also played a role in determining the patterns of diversity found today.

The results of the present study show that microenvironmental adaptation cannot be completely discarded as a possible factor in shaping craniofacial morphological variation in populations around the Indian Ocean rim. The overall pattern of diversity presented in Chapter 3 may be better explained by a combination of factors. Lahr (1996) stated that there is no clear empirical or theoretical evidence that points to environmental adaptation as a main factor in shaping craniofacial morphology in *Homo sapiens*. It is demonstrated, however, that environmental adaptation is a factor in the development of craniofacial diversity, even if it is not sufficient to state that the variables under study played a role in the origin of overall morphological differences. Environmental adaptation appears to be more correlated with specific areas of the craniofacial skeleton, with a limited effect on overall morphological shape. Local adaptation is acting on some aspects of variation that is not uniformly distributed across the craniofacial skeleton, as demonstrated by the differing level of effect of precipitation depending on whether the complete craniofacial skeleton is considered or only the variance described by PCs 3 and 8. Hypothesis $\mathbf{H_1}$, that relationships in craniofacial shape are not determined by current environmental variables, is therefore refuted. $\mathbf{H_2}$ stated that relationships in craniofacial size are not determined by current environmental variables. As no significant correlation is found between centroid size and any of the environmental factors studied, this hypothesis is therefore supported.

4.5.2 Summary of craniofacial shape variation and epigenetic factors

Both environment and isolation are known to play a small part in creating the craniofacial diversification of extant *Homo sapiens* (Howells, 1973; Guglielmino-Matessi *et al*, 1979; Hernández *et al.*, 1997). The results of the present chapter demonstrate that this holds true for the populations on and around the Indian Ocean rim. When total craniofacial shape is considered, variation is more clearly patterned by structural-historical aspects of the populations than by some important non-genetic differences such as temperature or rainfall. As shown in Chapter 3, the initial migration

of *Homo sapiens* out of Africa during the Late Pleistocene can be traced in the craniofacial variation found within the extant populations. A combination of the initial dispersal event and adaptation to local environments, have contributed to the diversity found today. Lahr (1996) suggested that early modern human populations most probably faced greatly differing environments, both spatially and temporally. The plastic nature of the craniofacial skeleton demonstrated in this chapter affirms this suggestion that local adaptations may have added to cranial diversity at each spatial and temporal step. Craniofacial morphological diversification will have thus emerged from the beginnings of human migratory history. Renaud (1999) stated that there is a complex relationship between morphological variation and phylogenetic constraints on one hand, and environmental variation on the other. To this should be added the effects of population movements, not only the original Late Pleistocene migration but all subsequent dispersals and adaptation to specific environmental conditions.

In this chapter craniofacial morphological diversity is analysed in a range of samples taken from on and around the Indian Ocean rim. The chapter concludes that a combination of geography and environmental factors act upon the patterns of variation found in the studied samples. Chapter 3 demonstrated that although limited in range, there are overall distinctive craniofacial shape differences between the populations studied. These results are particularly strong within regional groupings, adding to the suggestion that a combination of geography and environmental variables are acting on the patterns of variation found. As Roseman (2004) suggests, correlations between a putative selection pressure that is spatially distributed and patterns of biological diversity, may be due to a correlation between population structure and history and the spatial distribution of the putative selection pressure. Due to the regional groupings found in the studied samples, the following chapters will look specifically at the patterns of craniofacial variation within these regions to explore whether migratory history can be determined on a microevolutionary scale.

- Overall differences in temperature are correlated with biological distance

- PC1 is correlated with temperature

- PC3 is correlated with temperature and precipitation, reflecting a relationship between the variance described by this PC and latitude

- PC8, although explaining a small amount of variance, is influenced by precipitation and the length of the plant growing season, suggesting some as yet unidentified relationship with subsistence strategy. Further study would benefit from exploring this relationship with populations of known subsistence behaviour

- No correlation is found between any of the environmental variables and craniofacial size.

Chapter 5

Craniofacial Diversity in South and Southeast Asia

5.1 Introduction

Chapter 3 demonstrated that among the populations living around the Indian Ocean rim there is a significant pattern of regional clustering in cranial morphology. Two main regional groupings were identified, one around South and Southeast Asia and the other including Melanesia and Australia, both of which were selected for further study. This chapter will address morphological patterns and variation within the South and Southeast Asian region. There are two general themes prevalent to this region, the first concerning the biological relationship of present day Southeast Asians to their geographic neighbours in South and East Asia, Melanesia and Australia. The second theme concerns the so-called 'Negrito' populations, such as the Andaman Islanders, found within South and Southeast Asia, and their proposed evolutionary position as relics from the Late Pleistocene dispersal.

5.1.1 Craniofacial diversity in South and Southeast Asia

South Asia plays a central role in the southern coastal route hypothesis, acting as a corridor for the dispersal of *Homo sapiens* from Africa onwards into Southeast Asia, Melanesia and Australia. The region of South Asia includes the modern nations of India, Sri Lanka, Bangladesh, Nepal and Pakistan. Three major migrations of *Homo sapiens* into the Indian subcontinent have been postulated, starting with the Late Pleistocene dispersal from Africa. The exact date of the initial entry of *Homo sapiens* into South Asia is uncertain, though mtDNA coalescence times of the Indian specific branches of haplogroup M, suggest an early migration by at least 60,000 years ago (Kivisild *et al.*, 1999a, b; Quintana-Murci *et al.*, 1999). Archaeological evidence indicates that the entire Indian subcontinent was occupied during the Late Pleistocene, including the settlement of both coastal and estuarine environments (James and Petraglia, 2005). Skeletal remains from the Fa Hien Cave, Sri Lanka, dating to around 31,000 years ago, show the presence of *Homo sapiens* by at least this time (Deraniyagala, 1992). A second migration event occurred around 10,000 years ago, with the spread of proto-Dravidian speaking Neolithic farmers throughout

the region (Watkins *et al.*, 1999). Finally a third migration of Indo-European speaking 'Caucasoids', from West-Central Asia, entered around 3,500 years ago.

The diverse migrations into the subcontinent provide the potential for considerable morphological and genetic diversity within South Asia. It has been suggested that, with the exception of Africa, India harbours more genetic diversity than any other comparable global region (Majunder, 1998). Great cultural as well as biological diversity is found within the Indian subcontinent, with the population stratified as tribal and non-tribal groups. Although tribal groups, such as the Austro-Asiatic speaking Saora (Elwin, 1955) and the Tibeto-Burman speaking Lepcha (Van Dreim, 2001), constitute only about 8% of the total Indian population, they are generally considered to be the aboriginal inhabitants of the subcontinent (Cavalli-Sforza *et al.*, 1994). There is much debate regarding whether the genetic diversity found between different Indian populations primarily reflects their local long term differentiation, or is due to the different migrations mentioned above. The latter theory is supported by genetic studies that claim that results from the molecular data are congruent with linguistic diversity among regional tribes (Cavalli-Sforza *et al.*, 1992; Majumder, 1998). Roychoudhury *et al.* (2001) and Cordaux *et al.* (2004), for example, demonstrated that patterns of genomic diversity among the tribal populations inhabiting different geographic regions reflect heterogeneous origins of differing linguistic groups. Contrasting mtDNA studies, however, have suggested that the basic clustering of lineages is not linguistically defined or caste specific (Mountain *et al.*, 1995; Kivisild *et al.*, 1999a). The question of the origins of the patterns of genetic diversity seen between the diverse populations of India currently remains unresolved.

To progress from South Asia, into Melanesia and onto Australia, modern humans had first to pass through Southeast Asia. The dispersal of early migrants from India through Southeast Asia is suggested by studies of both mtDNA and Y chromosomes (Su *et al.*, 1999; Majumder, 2001). Southeast Asia is not a well defined homogeneous region in terms of either geography or biology. Geographically, the region consists of Myanmar (Burma), Thailand, Cambodia, Laos, Vietnam, Malaysia and the islands of Indonesia and the Philippines. Biologically, prior research indicates that the extant populations of Southeast Asia are morphologically diverse

(Lahr, 1996). Bowles (1977) went so far as to describe Southeast Asians as representing a human 'kaleidoscope'.

It has long been considered that Southeast Asia was originally occupied by indigenous people akin to the present day occupants of Melanesia and Australia (von Koenigswald, 1952; Coon, 1962; Bellwood, 1997). The origins of the present day Southeast Asian morphology, however, is still the subject of much debate. Two main models are proposed, the 'two-layer' or 'immigration' model and the 'regional continuity' or 'local evolution' model (Bellwood, 1997; Pietrusewsky, 2006). The 'two-layer' model favours population replacement and the interchange of genes as the reasons for the heterogeneous nature of the modern Southeast Asians (Bellwood, 1997). The model proposes replacement by or substantial genetic admixture of the indigenous population with East Asian immigrants, associated with the spread of agriculture from the Neolithic period onwards (Bellwood, 1997). In this scenario, the present day Southeast Asians would therefore represent a somewhat hybridised population. Evidence used to support this model includes archaeology and more particularly linguistics (Renfrew, 1992; Blust, 1996).

The second model, that of 'local evolution' argues for regional continuity within Southeast Asia. Proponents of the model state that the present day Southeast Asians represent the direct lineal descendents of the prehistoric population, without any significant admixture with East Asians until the present time (Turner, 1987, 1992; Hanihara, 1994). The evidence for this model comes mainly from studies of the skeletal remains of Southeast Asians, both prehistoric and modern. Hanihara (1993, 1994), for example, used craniometrics to support his hypothesis of local adaptation and argued that there is no evidence of an 'Australo-Melanesian' lineage in present day Southeast Asians. In a more recent study, Hanihara (2006) found that Southeast Asians and East Asians are not necessarily close to one another morphologically, thus arguing against the complete or nearly complete replacement hypothesis. Pietrusewsky (1999, 2006) also argues for regional continuity within Southeast Asia rather than displacement, and further suggests that there is rather a distinct dissimilarity between Southeast Asians and Australo-Melanesians.

Few examples of prehistoric human remains have been found in Southeast Asia, even though the evidence of early occupation in Melanesia and Australia indicates that Southeast Asia must have been traversed during the Late Pleistocene. Of the specimens that have been found, many are described as having similar morphological features to 'Australo-Melanesians', as suggested by the 'two-layer' model (Trevor and Brothwell, 1962; Matsumura, 2006). One of the earliest skeletons known from the region is that found at Moh Khiew Cave in Thailand, dated to c 25,800 ± 600 BP (Matsumura and Pookajorn, 2005). Morphometric analysis of the Moh Khiew skeleton has demonstrated close affinities with Australian samples in both cranial and dental data (Matsumura and Pookajorn, 2005). Analysis of the mtDNA from the skeleton, however, revealed continuity with the Semang Negrito foragers living today in the Malay Peninsula (Oota *et al.*, 2001). A sub-adult skull from the Niah cave in Sarawak, dated to approximately 40,000 years old (Kennedy, 1977), has similarly been compared to Tasmanian cranial morphology (Brothwell, 1960). Dental studies by Turner (1989, 1990, 1992) demonstrate that early and modern Southeast Asians display the so-called 'Sundadont' dental complex, shared with modern Australian Aborigines. Turner interprets this as demonstrating that Australian Aborigines and Southeast Asians originated from a common ancestral population inhabiting Sundaland during the late Pleistocene. Not all early remains from Southeast Asia, however, are interpreted as showing morphological similarities to modern 'Australo-Melanesians'. Storm (1995) examined the Wajak skulls from central Java, dating to about 6,500 BP, and found similarities to modern Indonesians rather than to Australians.

Hypotheses

The aim of this chapter is to explore the craniofacial morphology of Southeast Asians in relation to the proposed southern route and to assess whether aspects of the early dispersal from Africa can be identified. As Southeast Asia acted as a stepping stone from South Asia (Majumder, 2001; Su *et al.*, 1999), samples from the region will be compared with samples from the Indian subcontinent and the following null hypothesis is erected:

H_1 "The populations of Southeast Asia are not morphologically distinct in craniofacial shape from those of South Asia"

The hypothesis will be refuted if statistically significant differences in morphology are found between samples from the two regions.

One of the main debates surrounding the origins of the Southeast Asians concerns whether the pre-Neolithic occupants of Southeast Asia have an 'Australo-Melanesian' affinity. Admixture with or replacement by East Asians during the Holocene would suggest that no similarity would be found between the Southeast Asians and the Oceanic populations. Local evolution to the modern phenotype with no replacement would suggest more similarities between the Southeast Asians and the Australians and Melanesians. The Southeast Asian samples will therefore also be compared with samples from Melanesia and Australia to assess whether any affinity between these populations is present in modern morphology. The following null hypothesis is erected:

H_2 "The populations of Southeast Asia are not morphologically distinct in craniofacial shape from those of Melanesia and Australia"

The hypothesis will again be refuted if statistically significant differences between the regions are found.

5.1.2 'Relic' populations around the Indian Ocean rim

Having considered the nature of craniofacial diversity found within present day South and Southeast Asian populations, the chapter will address the issue of so-called 'relic' populations found within these two regions. It has been suggested that these 'relic' populations may be the direct descendents of the earliest dispersing population out of Africa, along with Papuans and Australian Aborigines (Nei and Roychoudhury, 1993; Macaulay *et al.*, 2005). Several groups from South and Southeast Asia have been postulated as possible 'relic' populations, including the Semang of the Malay Peninsula and the Aeta of the Philippines. Due to the limited availability of suitable skeletal samples, the proposed 'relic' populations represented

in this study are the Andaman Islanders, the Nicobar Islanders and the Veddah from Sri Lanka.

The people of the Andaman Islands possess the distinctive phenotype that is said to categorise the 'Negrito' populations found throughout Southeast Asia and Near Oceania. These features include short stature, dark skin pigmentation, peppercorn hair and sometimes steatopygia (Thangaraj *et al.*, 2003). The Andaman Islanders are thought to have been isolated from the outside world until the mid-19th century (Endicott *et al.*, 2003a) and their languages are considered part of the proposed Indo-Pacific language family found on New Guinea and New Britain (Whitehouse *et al.*, 2004). Andamanese crania have been likened to those of Africans (Howells, 1973), but genetic studies reveal closer affinities with Asian rather than African populations (Endicott *et al.*, 2003a; Thangaraj *et al.*, 2003). Molecular studies have suggested long term isolation, with a date of coalescence for mtDNA around 60,000 years ago (Endicott *et al.*, 2003a; Thangaraj *et al.*, 2003), though this has now been modified to a more recent date, possibly around 50,000 years ago (Thangaraj *et al.*, 2006). Geographically near to the Andaman Islands are the Nicobar Islands, whose inhabitants are also considered to be descendents of the early human dispersals into Southeast Asia (Cavalli-Sforza *et al.*, 1994). The Nicobar Islands speak languages linked to the Mon-Khmer languages of Cambodia and Vietnam, part of the Austro-Asiatic language family (Das, 1977). MtDNA analysis has linked the Nicobarese to populations of Southeast Asia, specifically with those of Cambodia (Prasad *et al.*, 2001) and a recent arrival from East Asia has been postulated during the past 18,000 years (Thangaraj *et al.*, 2005). The indigenous inhabitants of Sri Lanka, the Veddah, are thought to be the descendents of the first inhabitants of the island (Deraniyagala, 1992). The Veddah have been compared morphologically to other Southeast Asian 'Negrito' populations and also Australian Aborigines (Howells, 1959, 1993). Some interaction between the Veddah and the Singhalese seems likely, however, as the Veddah speak the Singhalese language which arrived in Sri Lanka over 2,000 years ago (Kennedy, 2003).

Hypotheses

A number of groups from South and Southeast Asia have thus been suggested as possible 'relic' populations of the initial migration out of Africa during the Late Pleistocene. These populations are said to share a common 'Negrito' morphology,

reflecting a shared descent from the first colonisers of South and Southeast Asia. In order to explore the possibility of these populations being 'relic' in terms of craniofacial morphology, the following null hypotheses are erected:

H_3 "The craniofacial skeleton of the Andaman Islanders is not significantly different from that of other South or Southeast Asian populations"

H_4 "The craniofacial skeleton of the Nicobar Islanders is not significantly different from that of other South or Southeast Asian populations"

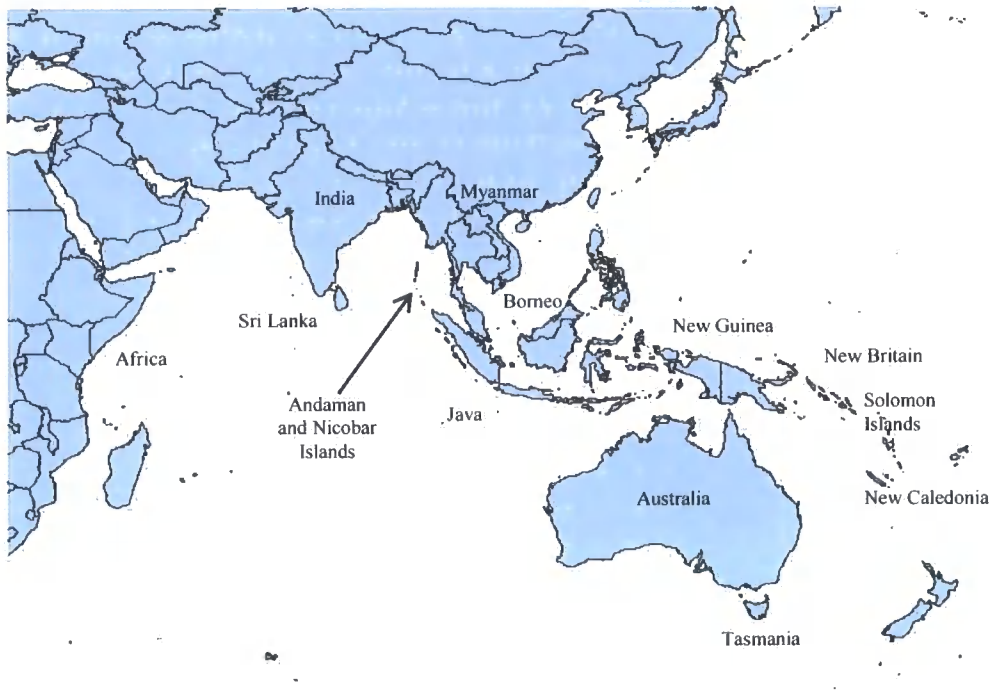
H_5 "The craniofacial skeleton of the Veddah is not significantly different from that of other South or Southeast Asian populations"

These hypotheses will be refuted if statistically significant differences are found in craniofacial shape between the three proposed 'relic' groups and all other South and Southeast Asian samples.

5.2 Materials

The 534 crania included in this chapter represent sub-sets of extant populations that are found in Africa, South Asia, Southeast Asia and Oceania. Samples marked ** are used only in the analyses of sample means, due to the small sample size. The samples are of mixed sex. Further details of each sample can be found in Chapter 2 (Materials and Methods).

Figure 5.1 Map of South and Southeast Asia, Melanesia and Australia



5.3 Methods used in this chapter

Biological Distances

The degree of discrimination in shape between the groups was measured using Mahalanobis' D for the complete samples in SAS (The SAS Institute Inc., 1996). Mahalanobis' D, or generalised distance, is a function of the group means and the pooled variances and covariances among populations. Mahalanobis' D is used to test whether group centroids are significantly different. To measure the differences between the means of population samples, Procrustes distances were utilised. The distance is approximately the square root of the sum of squared differences between the positions of the landmarks after General Procrustes Analysis (GPA).

Discriminant Analysis

Discriminant analysis with crossvalidation is used to classify individuals into predefined groups, based upon Mahalanobis' D^2 distances. Each individual is assigned a probability of belonging to a given group based on the distance of its discriminant function from that of each group mean. Crossvalidation is employed as it provides a better assessment of classification accuracy than standard discriminant analysis. During crossvalidation, classification is carried out for each individual in turn and the discriminant function used in each case is constructed with that individual removed. The crossvalidation analyses are carried out using SAS (The SAS Institute Inc., 1996).

Distance Phenograms

UPGMA phenograms were constructed on the basis of the paired Mahalanobis' distances in order to summarise the morphological relationships between the groups. The phenograms were created using the program NTSYS (Exeter Software).

Table 5.1 Composition of data sets

Region	Country	Sample	Sample Size	Specimen Location*
Africa				
	Kenya	Teita	35	DC
	Tanzania	Haya	35	DC
South Asia				
	India	Lepcha**	9	NHM
	India	Mysore**	9	NHM
	India	Bengal	35	NHM, DC
	India	Punjab	35	NHM, DC
	Sri Lanka	Sri Lanka	22	NHM, O, DC
	Sri Lanka	Veddah	15	NHM
Southeast Asia				
	Myanmar	Myanmar	35	DC
	Andaman Islands	Andaman Islands	34	NHM, DC
	Nicobar Islands	Nicobar Islands	13	NHM, DC
	Borneo	Borneo	35	NHM, O, DC
	Java	Java	17	NHM, O
	Sulawesi	Sulawesi**	5	NHM
	Moluccas	Moluccas**	6	NHM
	Sumatra	Sumatra**	6	NHM, DC
	Timor	Timor**	7	NHM
Melanesia				
	Papua New Guinea	Awaiama	19	DC
	Papua New Guinea	Kwaiawata	18	DC
	Papua New Guinea	Sinaugolo	21	NHM, DC
	New Britain	New Britain	35	NHM, DC
	Solomon Islands	Solomon Islands	21	NHM, O, DC
	New Caledonia	New Caledonia	15	NHM, DC

Australia				
	Australia	New South Wales	24	NHM, O, DC
	Australia	South Australia	16	NHM, O, DC
	Australia	Tasmania	12	NHM, O
TOTAL			**534**	

* NHM, Natural History Museum, London; O, The University Museum of Natural History, University of Oxford: DC, The Duckworth Laboratory, University of Cambridge.

** Used only in the analyses of sample means.

5.4 Results

5.4.1 Craniofacial diversity in South Asia and Southeast Asia

Principal components analysis is performed on the Procrustes fitted data from nine South and Southeast Asian samples and two African samples in order to compare craniofacial morphology between the regions. The principal components for the total sample variance are listed in table 5.2. PC1 explains 10.4% of the total sample variance and PC2 9.35%. As illustrated by figure 5.2, there is no clear separation of samples on PC1 and PC2, or on any single PC.

Figure 5.2. South and Southeast Asia: PC 1 v PC 2

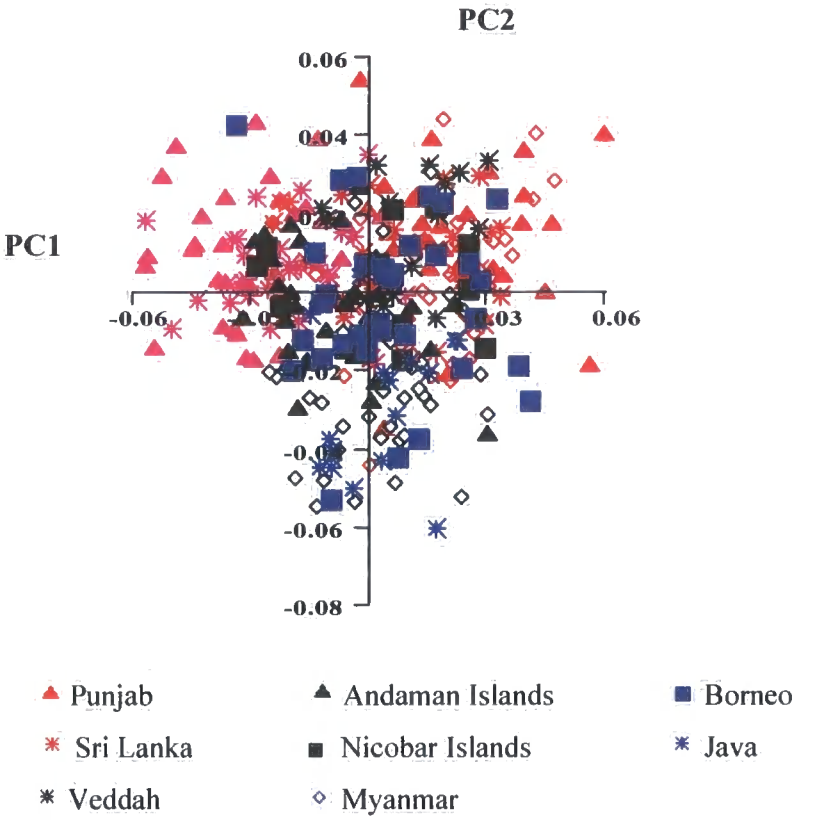


Table 5.2 South and Southeast Asia: The proportion of and accumulated variance of PCs 1 – 131, which account for almost 100% of total sample variance

PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %
1	10.40	10.40	**35**	0.62	82.61	**69**	0.20	95.03	**103**	0.06	99.02
2	9.35	19.75	**36**	0.61	83.22	**70**	0.20	95.22	**104**	0.06	99.08
3	6.85	26.60	**37**	0.60	83.81	**71**	0.19	95.41	**105**	0.06	99.13
4	4.82	31.42	**38**	0.56	84.37	**72**	0.18	95.59	**106**	0.05	99.19
5	4.66	36.08	**39**	0.55	84.91	**73**	0.17	95.77	**107**	0.05	99.24
6	4.04	40.12	**40**	0.53	85.44	**74**	0.17	95.94	**108**	0.05	99.29
7	3.36	43.48	**41**	0.51	85.96	**75**	0.16	96.10	**109**	0.05	99.34
8	3.18	46.66	**42**	0.49	86.45	**76**	0.16	96.26	**110**	0.05	99.39
9	2.96	49.62	**43**	0.48	86.92	**77**	0.15	96.42	**111**	0.04	99.43
10	2.70	52.32	**44**	0.47	87.39	**78**	0.15	96.56	**112**	0.04	99.47
11	2.40	54.72	**45**	0.42	87.81	**79**	0.15	96.71	**113**	0.04	99.52
12	2.17	56.89	**46**	0.41	88.22	**80**	0.14	96.84	**114**	0.04	99.56
13	2.04	58.93	**47**	0.40	88.62	**81**	0.13	96.98	**115**	0.04	99.60
14	1.89	60.82	**48**	0.38	89.00	**82**	0.13	97.11	**116**	0.04	99.63
15	1.76	62.58	**49**	0.38	89.38	**83**	0.12	97.23	**117**	0.03	99.67
16	1.63	64.21	**50**	0.37	89.75	**84**	0.12	97.35	**118**	0.03	99.70
17	1.54	65.75	**51**	0.37	90.12	**85**	0.12	97.47	**119**	0.03	99.73
18	1.45	67.20	**52**	0.35	90.47	**86**	0.11	97.58	**120**	0.03	99.76
19	1.35	68.55	**53**	0.35	90.81	**87**	0.11	97.69	**121**	0.03	99.79
20	1.27	69.82	**54**	0.33	91.14	**88**	0.11	97.80	**122**	0.03	99.82
21	1.20	71.02	**55**	0.33	91.47	**89**	0.10	97.90	**123**	0.03	99.84
22	1.11	72.13	**56**	0.32	91.79	**90**	0.10	98.00	**124**	0.02	99.87
23	1.03	73.16	**57**	0.31	92.10	**91**	0.10	98.10	**125**	0.02	99.89
24	1.00	74.16	**58**	0.29	92.39	**92**	0.09	98.19	**126**	0.02	99.91
25	0.95	75.11	**59**	0.28	92.67	**93**	0.09	98.28	**127**	0.02	99.93
26	0.93	76.04	**60**	0.28	92.95	**94**	0.09	98.37	**128**	0.02	99.95
27	0.90	76.94	**61**	0.26	93.21	**95**	0.08	98.45	**129**	0.02	99.97
28	0.81	77.74	**62**	0.26	93.46	**96**	0.08	98.53	**130**	0.02	99.99
29	0.79	78.53	**63**	0.25	93.71	**97**	0.08	98.61	**131**	0.02	100.00
30	0.73	79.26	**64**	0.24	93.94	**98**	0.07	98.69			
31	0.70	79.97	**65**	0.23	94.18	**99**	0.07	98.76			
32	0.70	80.67	**66**	0.23	94.40	**100**	0.07	98.83			
33	0.67	81.33	**67**	0.22	94.62	**101**	0.06	98.89			
34	0.65	81.98	**68**	0.21	94.83	**102**	0.06	98.96			

To eliminate the effects of noise factors such as intra-population variation on the data, separate discriminant analyses are performed using differing amounts of variance. The results are given in table 5.3, and show that the best discrimination is found using approximately 95% of the total sample variance. All further analyses in this section are therefore performed using PCs 1-69. The Mahalanobis' distances between the sample groups are given in table 5.4. All distances are statistically significant. The smallest distance ($D = 9.38$; $p = 0.0004$) is found between the samples from Bengal and the Punjab, and the largest between the Teita and Nicobar Islands samples ($D = 67.80$; $p < 0.001$).

Table 5.3 South and Southeast Asia: Cross validation study to assess the separation by proportion of sample variance. Numbers indicate % correctly assigned.

Sample	**70%** (PCs 1-20)	**80%** (PCs 1-31)	**90%** (PCs 1-51)	**95%** (PCs 1-69)	**100%** (PCs 1-138)
Teita	68.57	71.43	80.00	80.00	77.14
Haya	88.57	88.57	85.71	82.86	85.71
Ben	40.00	40.00	37.14	48.57	42.86
Pun	68.57	68.57	68.57	60.00	57.14
SL	36.36	36.36	27.27	45.45	36.36
Ved	66.67	53.33	53.33	53.33	26.67
Mya	68.57	74.29	80.00	85.71	68.57
And	82.35	79.41	88.24	91.18	79.41
Nic	69.23	84.62	92.31	92.31	61.54
Bor	51.436	62.86	60.00	57.14	71.43
Java	70.59	64.71	88.24	76.47	76.47
Mean	**64.63**	**65.83**	**68.26**	**70.27**	**62.12**

Table 5.4 Mahalanobis' D distance matrix; South and Southeast Asia; * significant at $p \leq 0.05$
Ben, Bengal; Pun, Punjab; SL, Sri Lanka; Ved, Veddah; Mya, Myanmar; And, Andaman Islands; Nic, Nicobar Islands; Bor, Borneo; Java, Java.

	Teita	Haya	Ben	Pun	SL	Ved	Mya	And	Nic	Bor	Java
Teita	0.00										
Haya	32.84*	0.00									
Ben	44.70*	35.80*	0.00								
Pun	57.37*	45.76*	9.38*	0.00							
SL	40.64*	33.39*	11.34*	17.46*	0.00						
Ved	48.53*	29.22*	14.23*	22.22*	19.24*	0.00					
Mya	45.22*	44.98*	29.28*	39.42*	29.33*	38.82*	0.00				
And	44.75*	41.24*	26.62*	44.33*	30.29*	36.14*	44.16*	0.00			
Nic	67.80*	66.12*	48.22*	52.71*	54.35*	47.26*	51.55*	60.32*	0.00		
Bor	41.28*	36.67*	20.16*	25.03*	21.90*	25.93*	24.39*	28.44*	34.22*	0.00	
Java	61.66*	64.58*	33.47*	39.51*	38.57*	42.50*	39.85*	42.95*	45.82*	19.80*	0.00

The results of the crossvalidation analyses are presented in table 5.5. Using 95% of the total sample variance resulted in 70.27% of all individuals being classified into their original groups. The lowest percentage of correctly classified individuals comes from the Sri Lankan sample with only 45.45%, with 50% misclassified into the remaining South Asian samples. The Nicobar Islands sample achieves the greatest amount of correct classification at 92.31%.

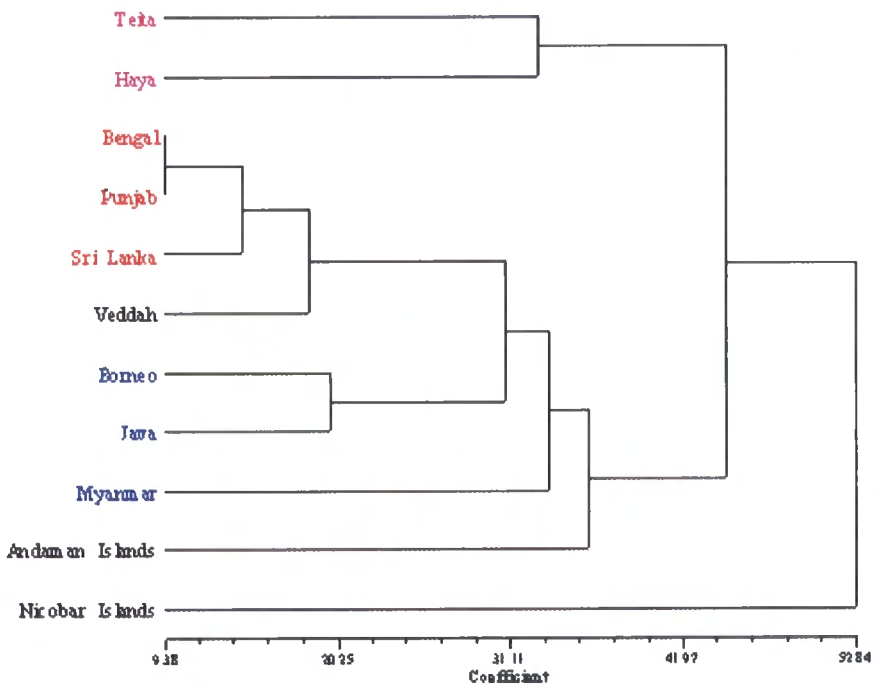
Table 5.5 Cross validation analysis: South and Southeast Asia

Ben, Bengal; Pun, Punjab; SL, Sri Lanka; Ved, Veddah; Mya, Myanmar; And, Andaman Islands; Nic, Nicobar Islands; Bor, Borneo; Java, Java.

	Teita	Haya	Ben	Pun	SL	Ved	Mya	And	Nic	Bor	Java	Total
Teita %	**80.00**	11.43	2.86	0.00	2.86	0.00	2.86	0.00	0.00	0.00	0.00	100.00
Haya %	2.86	**82.86**	0.00	0.00	0.00	8.57	0.00	2.86	0.00	2.86	0.00	100.00
Ben %	0.00	0.00	**48.57**	22.86	8.57	8.57	2.86	5.71	0.00	2.86	0.00	100.00
Pun %	0.00	2.86	25.71	**60.00**	8.57	0.00	0.00	0.00	0.00	2.86	0.00	100.00
SL %	0.00	9.09	27.27	4.55	**45.45**	9.09	0.00	0.00	0.00	0.00	4.55	100.00
Ved %	0.00	0.00	26.67	13.33	6.67	**53.33**	0.00	0.00	0.00	0.00	0.00	100.00
Mya %	0.00	2.86	5.71	0.00	2.86	0.00	**85.71**	0.00	0.00	2.86	0.00	100.00
And %	0.00	0.00	2.94	0.00	0.00	0.00	0.00	**91.18**	0.00	5.88	0.00	100.00
Nic %	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**92.31**	7.69	0.00	100.00
Bor %	0.00	0.00	5.71	0.00	5.71	0.00	5.71	5.71	2.86	**57.14**	17.14	100.00
Java %	0.00	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	17.65	**76.47**	100.00

A UPGMA phenogram providing a two dimensional illustration of the multidimensional craniofacial shape relationships between the samples is given in figure 5.3. The Nicobar Islands sample is the first to be separated from all other samples. Following this separation, two main branches are observed with the two African samples situated on one bifurcation and all remaining samples clustered on the other. Within this South and Southeast Asian cluster, the Andaman Islands sample is the first to be separated, followed by the Myanmar sample. Of the remaining samples, the South Asian samples form a separate cluster and the Borneo and Java samples form a second cluster (figure 5.3).

Figure 5.3 Phenogram showing relationships between the full South and Southeast Asian samples.



5.4.1a Craniofacial diversity in South Asia and Southeast Asia: Means

South and Southeast Asian craniofacial diversity is further explored using the sample means. The samples include those from the preceding section with the addition of samples which were too small to be included in the previous analyses. From South Asia, Lepcha and Mysore samples are added and from Southeast Asia samples from Sulawesi, the Moluccas, Sumatra and Timor. The African samples are not included in this set of analyses. The sample means are submitted to Procrustes fitting and PCA. PC1 and PC2 are shown in figure 5.4. Table 5.6 lists the percentage variance and cumulative variance explained by each PC. PC1 explains 36.7% of the total sample variance and PC2 11.8%.

Table 5.6 South and Southeast Asia sample means: The proportion and accumulated variance of PCs 1 – 14, which account for 100% of total sample variance

Principal Component	Variance %	Cumulative Variance %
1	36.70	36.70
2	11.80	48.50
3	10.90	59.40
4	8.37	67.77
5	5.95	73.72
6	5.04	78.76
7	4.93	83.69
8	4.31	88.00
9	3.29	91.29
10	2.57	93.86
11	2.15	96.01
12	1.84	97.85
13	1.50	99.35
14	0.65	100.00

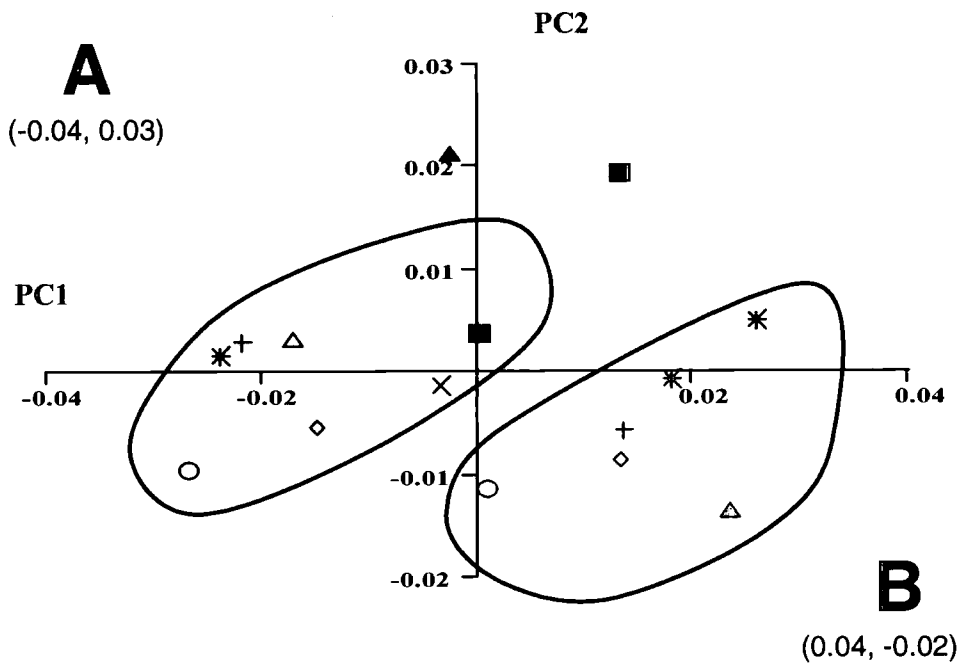
As illustrated by figure 5.4, PCs 1 and 2 separate the populations into two main clusters (circled), one containing samples from South Asia and the other from

Southeast Asia. Of the supposed 'relic' populations, marked in black on figure 5.4, the Veddah sit within the South Asian cluster whilst the Andaman and Nicobar Islands samples are situated as outliers from the two main clusters. The morphology of the Andaman and Nicobar Islanders appear to be driving the variance along PC2. No further meaningful clustering of populations is found on the remaining PCs.

Figure 5.5 shows the mean configuration warped to positions **A** (-0.04, 0.05) and **B** (0.04, -0.02) on PCs 1 and 2, respectively to illustrate the morphological difference between the South and Southeast Asian clusters. At **A**, the configuration has a relatively posteriorly sloping face (figure 5.5 i) contrasting with the relatively flatter face at **B**, where glabella is relatively more anteriorly positioned (figure 5.5 ii), the alveolar surface is relatively more posteriorly situated (figure 5.5 iii) and there is more relative mid face projection (figure 5.5 iv). At **B**, the face also appears relatively more compact than **A**, with stephanion relatively more anterioinferiorly placed (figure 5.5 v) and lambda and inion relatively more posteriorly and inferiorly situated (figure 5.5 vi).

Figures 5.6 shows the morphological changes along PC2. Warping from the negative to the positive extreme, where the Andaman and Nicobar Islanders are situated, the changes are mainly concentrated in the lower maxillary region. The alveolar surface is positioned relatively more anteriorly and there is much greater prognathism in the lower maxilla (figure 5.6 i).

Figure 5.4. South and Southeast Asians - means: PC 1 v PC 2



◇ Bengal
+ Mysore
■ Borneo
+ Moluccas
△ Punjab
✳ Veddah
✳ Java
× Sumatra
✳ Sri Lanka
▲ Andaman Islands
◇ Myanmar
△ Timor
○ Lepcha
■ Nicobar Islands
○ Sulawesi

Figure 5.5 South and Southeast Asia means. TPS of the shapes at positions A (-0.04, 0.05) and B (0.04, -0.02) illustrating the differences between the two shapes

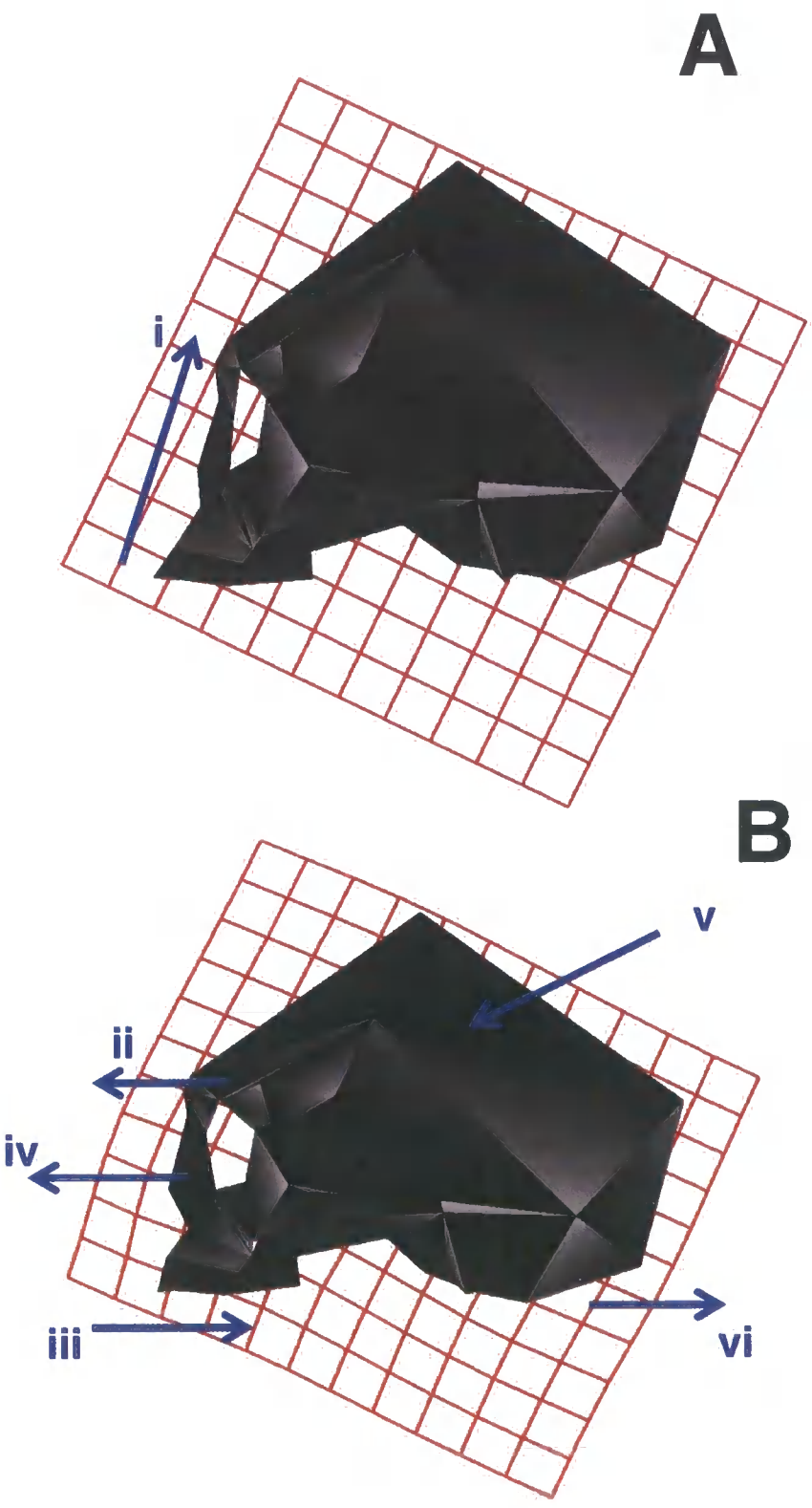
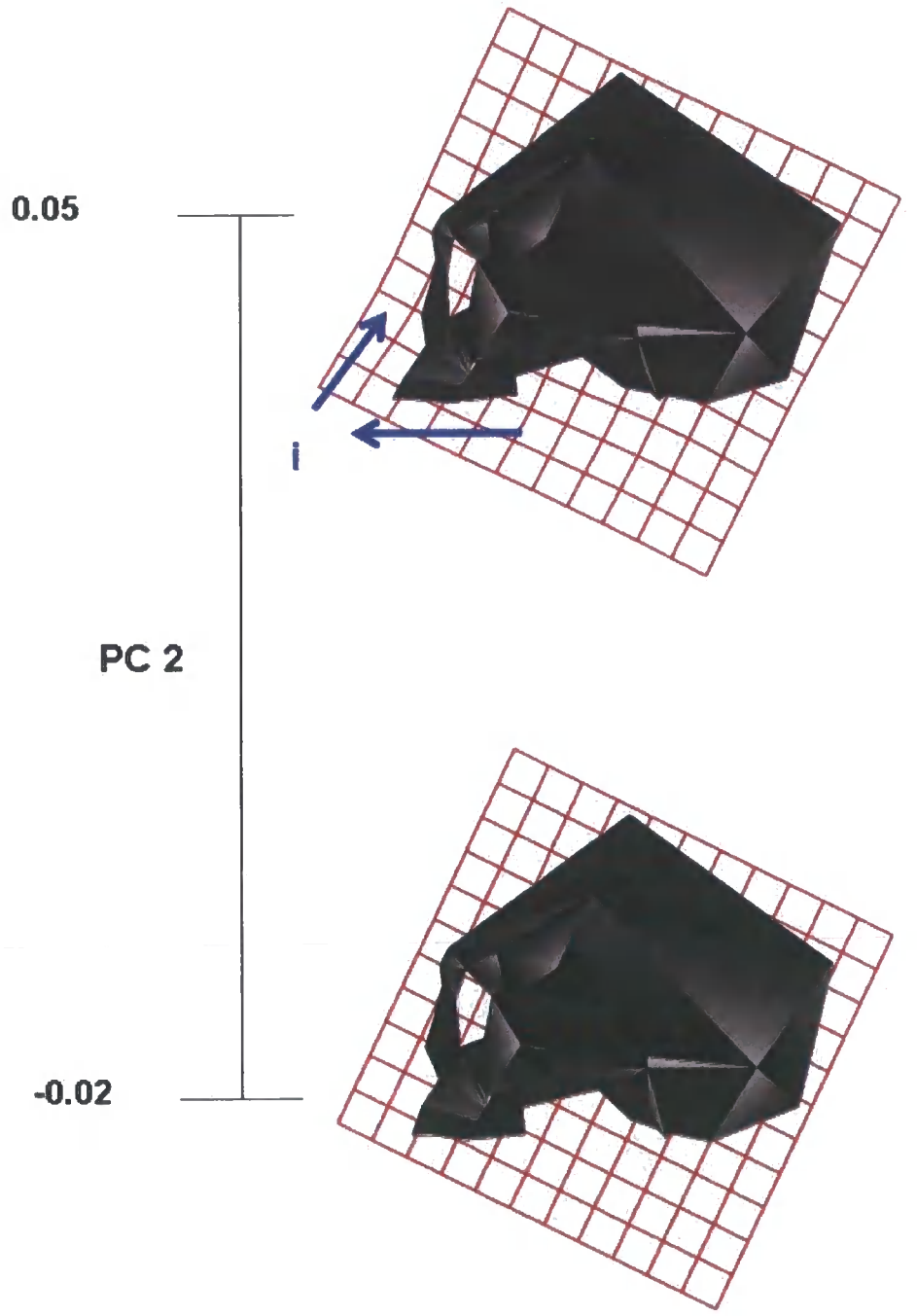


Figure 5.6 PC2 TPS: Differences in shape along the second PC. The upper figure represents the mean landmark configuration warped along PC2 from the negative to the positive extreme.



5.4.2 Craniofacial diversity in Southeast Asia and Australia/Melanesia

In order to address the second null hypothesis, that the populations of Southeast Asia are not morphologically distinct from those of Melanesia and Australia, the Procrustes fitted data from the combined regions are submitted to PCA. The principal components accounting for the total sample variance are listed in table 5.7. PC1 explains 11.2% of the total sample variance and PC2 7.7%. As with the South and Southeast Asian analyses, no clear separation of samples can be observed on PCs 1 and 2 (figure 5.7), or on any single higher PC.

Figure 5.7. Southeast Asia and Oceania: PC 1 v PC 2:

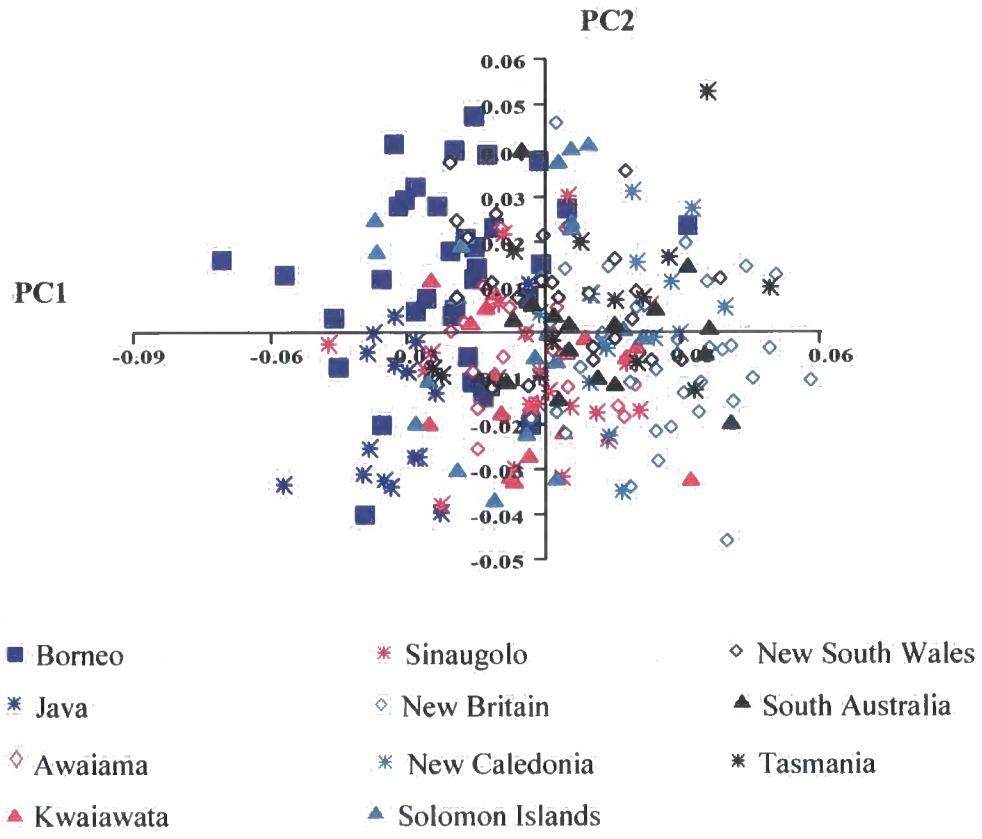


Table 5.7 Southeast Asia and Oceania: The proportion of and accumulated variance of PCs 1 – 134, which account for almost 100% of total sample variance

PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %
1	11.20	11.20	**35**	0.67	82.24	**69**	0.20	95.22	**103**	0.05	99.13
2	7.66	18.86	**36**	0.66	82.90	**70**	0.20	95.41	**104**	0.05	99.19
3	7.29	26.15	**37**	0.61	83.51	**71**	0.19	95.61	**105**	0.05	99.24
4	5.56	31.71	**38**	0.60	84.12	**72**	0.19	95.79	**106**	0.05	99.28
5	4.53	36.24	**39**	0.58	84.70	**73**	0.18	95.97	**107**	0.04	99.33
6	3.94	40.18	**40**	0.57	85.27	**74**	0.17	96.15	**108**	0.04	99.37
7	3.26	43.44	**41**	0.56	85.83	**75**	0.17	96.32	**109**	0.04	99.41
8	3.11	46.55	**42**	0.52	86.35	**76**	0.16	96.48	**110**	0.04	99.45
9	2.86	49.41	**43**	0.49	86.84	**77**	0.16	96.63	**111**	0.04	99.49
10	2.68	52.09	**44**	0.48	87.32	**78**	0.15	96.78	**112**	0.04	99.53
11	2.42	54.51	**45**	0.46	87.78	**79**	0.14	96.92	**113**	0.03	99.56
12	2.20	56.71	**46**	0.45	88.24	**80**	0.14	97.06	**114**	0.03	99.60
13	1.92	58.63	**47**	0.43	88.67	**81**	0.14	97.20	**115**	0.03	99.63
14	1.79	60.42	**48**	0.42	89.09	**82**	0.13	97.33	**116**	0.03	99.66
15	1.68	62.10	**49**	0.41	89.50	**83**	0.13	97.46	**117**	0.03	99.69
16	1.58	63.68	**50**	0.40	89.90	**84**	0.13	97.58	**118**	0.03	99.71
17	1.50	65.18	**51**	0.37	90.27	**85**	0.12	97.70	**119**	0.03	99.74
18	1.37	66.55	**52**	0.36	90.63	**86**	0.11	97.81	**120**	0.02	99.76
19	1.28	67.83	**53**	0.35	90.98	**87**	0.11	97.92	**121**	0.02	99.79
20	1.23	69.06	**54**	0.33	91.31	**88**	0.10	98.02	**122**	0.02	99.81
21	1.19	70.25	**55**	0.33	91.64	**89**	0.10	98.12	**123**	0.02	99.83
22	1.13	71.38	**56**	0.32	91.95	**90**	0.10	98.21	**124**	0.02	99.85
23	1.08	72.46	**57**	0.31	92.26	**91**	0.09	98.30	**125**	0.02	99.86
24	1.01	73.47	**58**	0.30	92.56	**92**	0.09	98.39	**126**	0.02	99.88
25	0.98	74.45	**59**	0.29	92.85	**93**	0.09	98.48	**127**	0.01	99.89
26	0.92	75.37	**60**	0.28	93.13	**94**	0.08	98.56	**128**	0.01	99.91
27	0.86	76.23	**61**	0.27	93.40	**95**	0.07	98.63	**129**	0.01	99.92
28	0.84	77.07	**62**	0.26	93.65	**96**	0.07	98.70	**130**	0.01	99.93
29	0.83	77.90	**63**	0.25	93.91	**97**	0.07	98.77	**131**	0.01	99.94
30	0.80	78.69	**64**	0.24	94.14	**98**	0.07	98.84	**132**	0.01	99.95
31	0.75	79.44	**65**	0.23	94.37	**99**	0.07	98.90	**133**	0.01	99.96
32	0.73	80.16	**66**	0.22	94.60	**100**	0.06	98.97	**134**	0.01	99.97
33	0.72	80.88	**67**	0.22	94.81	**101**	0.06	99.02			
34	0.70	81.58	**68**	0.20	95.02	**102**	0.06	99.08			

To examine the effects of noise from non-population specific factors, five separate discriminant analyses are performed and the results given in table 5.8. The best discrimination between samples is achieved using approximately 80% of the total sample variance and the remaining analyses in this section will therefore be performed using PCs 1 - 32. The Mahalanobis' distances between the sample groups are given in table 5.9. All distances are statistically significant. The largest distance is found between the Java and South Australian samples ($D=32.38$, $p < 0.001$) and the shortest between the Borneo and Kwaiawata samples ($D=7.55$, $p=0.003$).

Table 5.8 Southeast Asia and Oceania: Cross validation study to assess the separation by proportion of sample variance

Sample	**70%** (PCs 1-21)	**80%** (PCs 1-32)	**90%** (PCs 1-52)	**95%** (PCs 1-68)	**100%** (PCs 1-138)
Bor	71.43	60.00	62.86	60.00	42.86
Java	58.82	58.82	64.71	64.71	70.59
ANG	63.16	63.16	68.42	63.16	36.84
KNG	38.89	44.44	22.22	44.44	33.33
Sin	33.33	38.10	57.14	47.62	42.86
NB	74.29	85.71	82.86	71.43	48.57
SI	38.10	42.86	52.38	57.147	38.10
NC	40.00	46.67	53.33	60.00	20.00
NSW	50.00	66.67	58.33	62.50	58.33
SA	62.50	56.25	56.25	43.75	43.75
Tas	41.67	58.33	41.67	41.67	25.00
Mean	**52.02**	**56.46**	**56.38**	**56.04**	**41.84**

Table 5.9 Mahalanobis D' distance matrix: South and Southeast Asia; * significant at p<0.05

Bor, Borneo; Java, Java; ANG, Awaiama; KNG, Kwaiawata; Sin; Sinaugolo; NB, New Britain; SI, Solomon Islands; NC, New Caledonia; NSW, New South Wales; SA, South Australia; Tas, Tasmania.

	Bor	Java	ANG	KNG	Sin	NB	SI	NC	NSW	SA	Tas
Bor	0.00										
Java	7.69*	0.00									
ANG	15.05*	15.99*	0.00								
KNG	7.55*	9.77*	10.94*	0.00							
Sin	12.24*	13.71*	9.85*	9.51*	0.00						
NB	24.94*	30.86*	22.14*	17.47*	18.37*	0.00					
SI	12.98*	20.14*	17.00*	10.83*	9.10*	14.33*	0.00				
NC	21.71*	25.26*	15.73*	14.19*	18.58*	10.45*	20.33*	0.00			
NSW	20.18*	22.66*	18.98*	15.86*	13.40*	19.39*	11.64*	22.14*	0.00		
SA	29.18*	32.38*	27.31*	20.48*	19.05*	20.87*	16.76*	28.26*	10.45*	0.00	
Tas	16.19*	23.73*	19.41*	17.70*	13.80*	22.40*	13.10*	30.19*	12.96*	10.74*	0.00

Table 5.10 presents the results of the crossvalidation analyses of the samples. The highest percentage of correct classification is achieved by the New Britain sample, with 85.71% of the individuals being placed in the correct group. The lowest percentage of correct classification is achieved by the Sinaugolo sample, with only 38.1% of individuals being placed in their original group. The misplaced individuals from this group are alternatively placed in the Awaiama and Solomon Island samples.

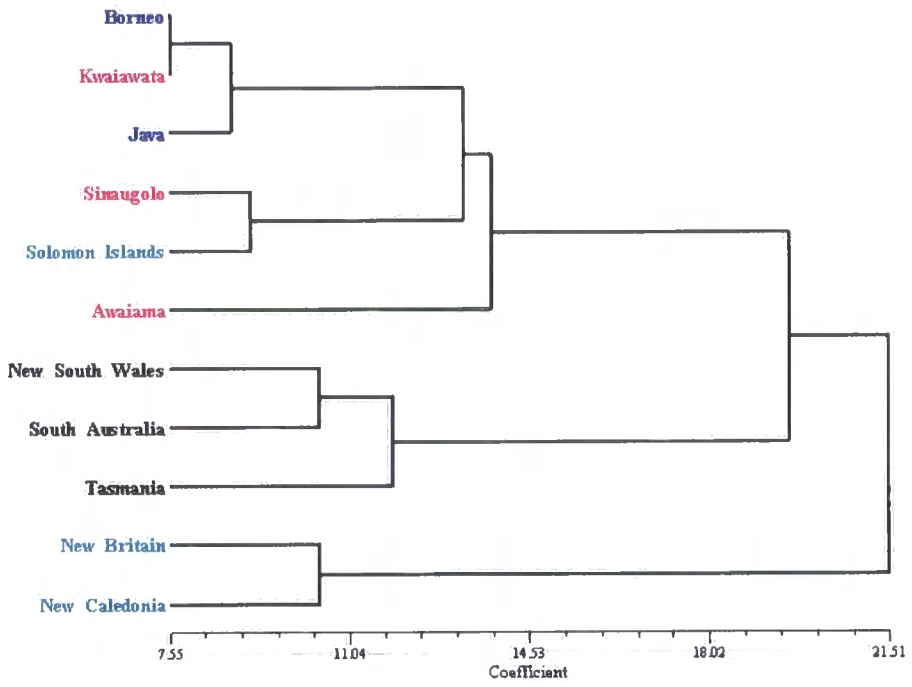
Table 5.10 Cross validation analysis: South and Southeast Asia

Bor, Borneo; Java, Java; ANG, Awaiama; KNG, Kwaiawata; Sin; Sinaugolo; NB, New Britain; SI, Solomon Islands; NC, New Caledonia; NSW, New South Wales; SA, South Australia; Tas, Tasmania.

	Bor	Java	ANG	KNG	Sin	NB	SI	NC	NSW	SA	Tas	**Total**
Bor%	**60.00**	17.14	2.86	8.57	2.86	2.86	2.86	2.86	0.00	0.00	0.00	100.00
Java %	11.76	**58.82**	5.88	11.76	0.00	0.00	5.88	0.00	0.00	0.00	5.88	100.00
ANG%	10.53	0.00	**63.16**	10.53	10.53	0.00	5.26	0.00	0.00	0.00	0.00	100.00
KNG %	11.11	5.56	0.00	**44.44**	16.67	0.00	11.11	5.56	0.00	0.00	5.56	100.00
Sin %	4.76	4.76	19.05	4.76	**38.10**	0.00	23.81	0.00	4.76	0.00	0.00	100.00
NB %	2.86	0.00	0.00	0.00	2.86	**85.71**	0.00	8.57	0.00	0.00	0.00	100.00
SI %	0.00	0.00	0.00	9.52	9.52	9.52	**42.86**	0.00	19.05	0.00	9.52	100.00
NC %	0.00	0.00	6.67	13.33	6.67	26.67	0.00	**46.67**	0.00	0.00	0.00	100.00
NSW %	0.00	0.00	8.33	0.00	0.00	0.00	8.33	4.17	**66.67**	4.17	8.33	100.00
SA %	0.00	0.00	0.00	0.00	6.25	6.25	0.00	0.00	12.50	**56.25**	18.75	100.00
Tas %	0.00	8.33	0.00	0.00	8.33	0.00	8.33	0.00	0.00	16.67	**58.33**	100.00

Figure 5.8 illustrates a UPGMA phenogram based upon the Mahalanobis' distances between the samples. The New Britain and New Caledonian samples are placed together within a separate cluster away from all the remaining samples. The second bifurcation of the phenogram separates off the three Australian samples. The two Southeast Asian samples are placed within the final cluster, on a separate branch along with the Kwaiawata sample from New Guinea. The remaining Melanesian sample, from the Solomon Islands, is also placed within this cluster, positioned on a branch with the Sinaugolo sample.

Figure 5.8 Phenogram showing distances between Southeast Asia and Oceania samples.



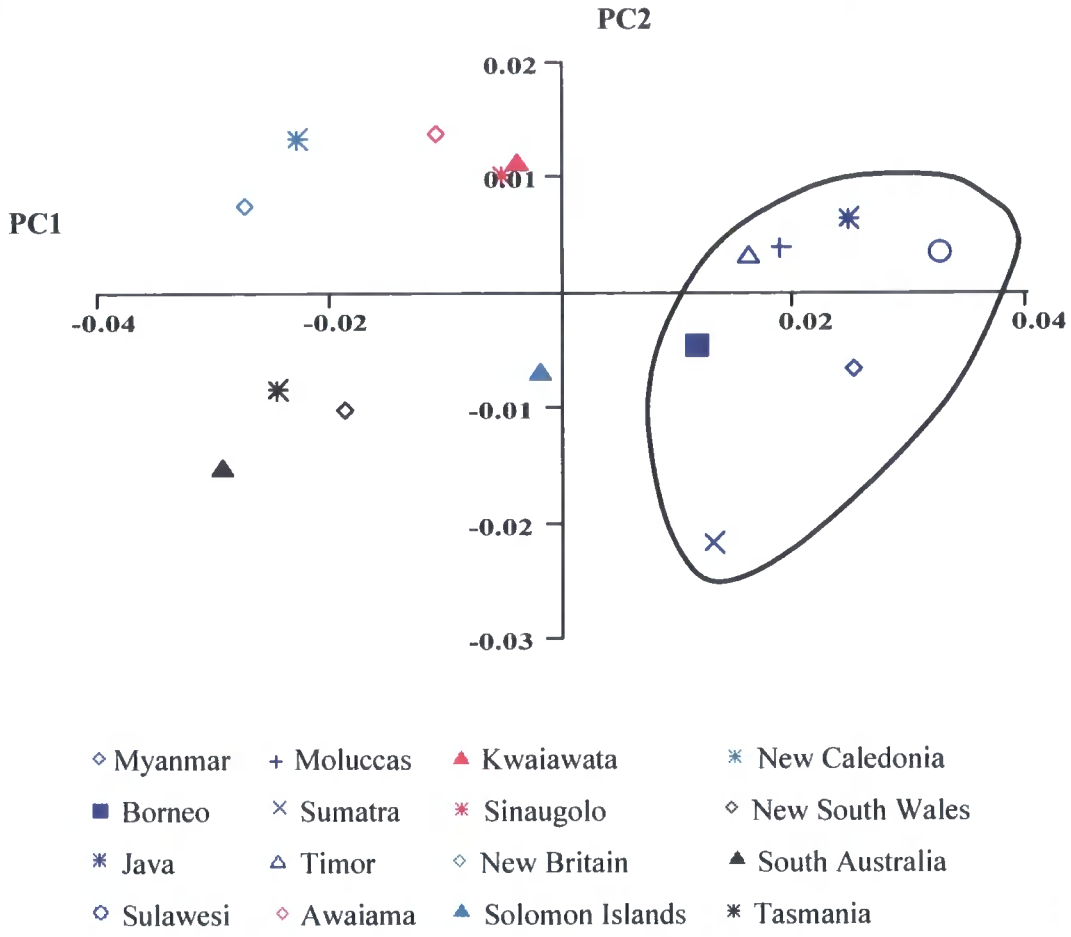
5.4.2a Craniofacial diversity in Southeast Asia, Melanesia and Australia: Means

Mean samples from Sulawesi, the Moluccas, Sumatra and Timor were added to the means of the samples analysed in section 5.4.3 and together were submitted to Procrustes analysis. A separation of the Southeast Asian samples from those of Melanesia and Australia can be seen along PC1 (figure 5.9). PC1 explains approximately 43.8% of the total sample variance, compared with only 11.7% on PC2. The percentage variance and cumulative variance explained by each PC is given in table 5.11. No meaningful separation of samples is given by PC2 or any further single PC.

Table 5.11 Southeast Asia and Oceania sample means: The proportion and accumulated variance of PCs 1 – 15, which account for 100% of total sample variance

Principal Component	Variance %	Cumulative Variance %
1	43.80	43.80
2	11.70	55.50
3	9.23	64.73
4	6.37	71.10
5	5.19	76.29
6	4.41	80.70
7	3.89	84.59
8	3.37	87.96
9	2.65	90.61
10	2.29	92.90
11	1.96	94.86
12	1.71	96.57
13	1.35	97.92
14	1.14	99.06
15	0.94	100.00

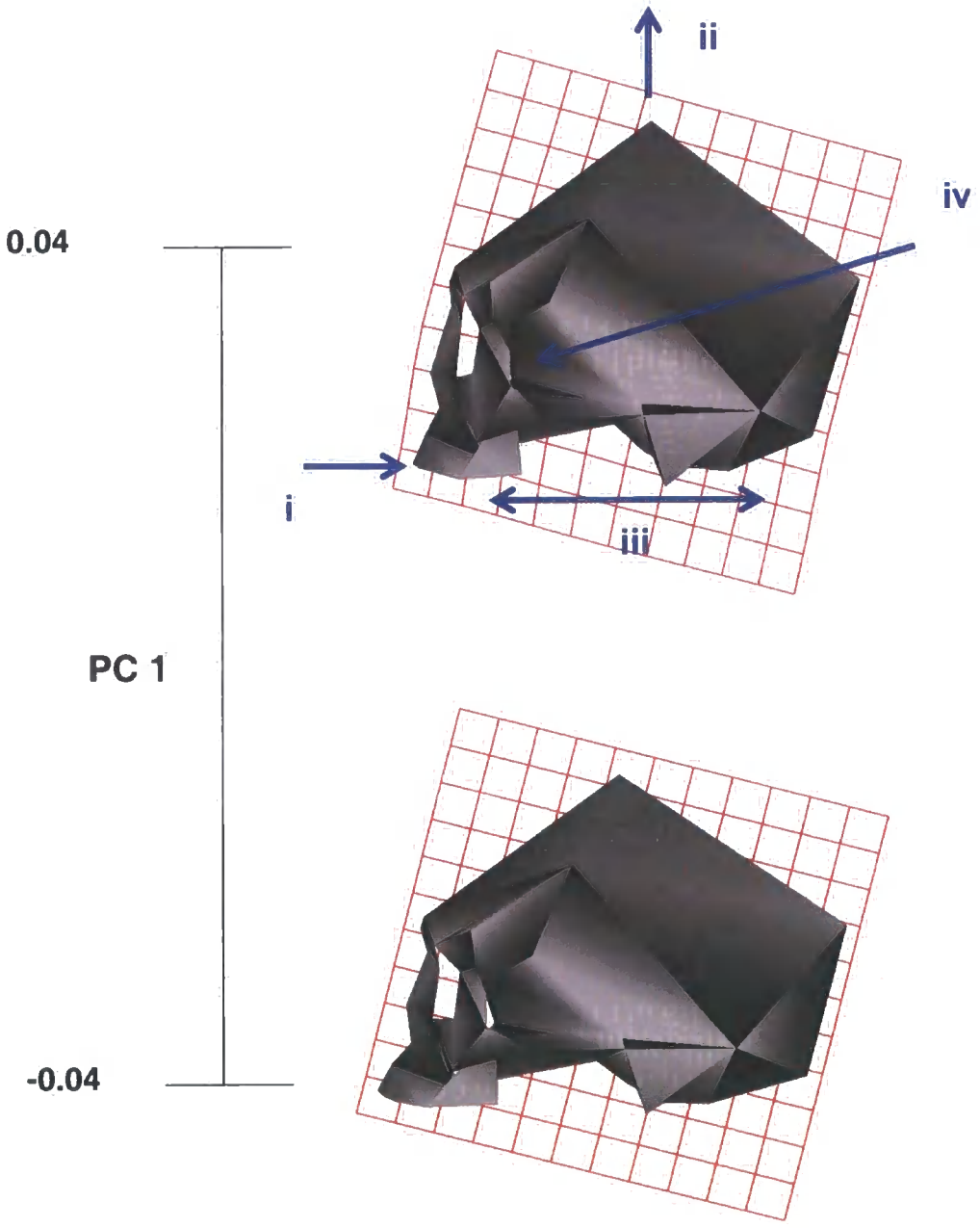
Figure 5.9. Southeast Asia and Oceania means: PC 1 v PC 2



The morphological variation along PC1 is defined by the differences between the Southeast Asians (circled), situated on the positive extreme of PC1, and the Australian and Melanesian samples that are situated towards the negative extreme (figure 5.9). Figure 5.10 shows the mean shape configuration at the negative and positive extremes of PC1, reflecting the differences in craniofacial morphology between the Australian and Melanesian samples and those from Southeast Asia. The main difference between the figures is the relatively increased height of the face and cranium at the positive extreme, with a more postero-inferior position of the alveolar surface (figure 5.10 i) along with a relatively more superior placement of bregma (figure 5.10 ii). The mean shape at the positive extreme of PC1 also has a relative decrease in basicranial length (figure 5.10 iii), with lambda and inion relatively more

anteriorly positioned. At the positive extreme of PC1 the face and cranium are also relatively wider than at the negative extreme, with a relative lateral displacement of stephanion and the zygomatic arch (figure 5.10 iv).

Figure 5.10 PC1 TPS: Differences in shape along the first PC. The upper figure represents the mean landmark configuration warped along PC1 from the negative to the positive extreme.



5.5 Discussion

5.5.1 Craniofacial diversity in South and Southeast Asia

The Indian subcontinent is characterised by great cultural and genetic diversity (Majumder, 1998). The results of this chapter show that craniofacial diversity is also demonstrable between samples from different South Asian localities, as shown by the significant Mahalanobis' distances given in table 5.4. Although the separate samples are diverse, the presence of a general South Asian morphology remains evident. This is demonstrated in the analyses by the clustering of the South Asian samples on both the phenogram (figure 5.3) and on PCs 1 and 2 of the sample means analysis (figure 5.4). Research on the genetics of South Asian populations has not reached a consensus over whether the diversity found is the product of the various migrations into the subcontinent (Cordaux *et al.*, 2004) or the result of local long term differentiation (Kivisild *et al.*, 2003). Although not conclusive, the results of the present study appear to support the idea that differentiation has come about due to long term occupation of the region rather than the introduction of new phenotypes due to migrations of specific linguistic groups. A general South Asian cranial morphology is suggested, with samples from the north to the south of the subcontinent, including Sri Lanka, showing more similarity to one another than to samples from Southeast Asia and Africa. A regional morphology may, of course, be created by gene flow between the indigenous inhabitants and any immigrant groups into the region. In the case of India this could be rejected due to the strongly stratified society based on the caste system, leading to a rigid hierarchical structure of the population (Das *et al.*, 2002). The gene pool is also restricted within India due to the endogamous nature of breeding within a socially and culturally specified group (Das *et al.*, 2002). It seems likely, therefore, that the pattern of diversity found within South Asia is due to a diversification from a common South Asian morphology over a long period of occupation, with only limited influence from external populations. A greater number of Indian samples and the inclusion of samples from the proposed migrant regions would be required to confirm or reject this finding.

South Asia is often referred to as an important corridor in the southern dispersal route from Africa during the Late Pleistocene. The aim of this chapter was to explore the craniofacial morphology of South Asians in relation to this link between

Africa and Southeast Asia. The results of the analyses, however, determine that there are distinct differences between the samples from the three regions assessed in section 5.4.1. The two African samples are clearly distinct from the South Asians, forming a separate cluster on the phenogram (figure 5.3) and achieving over 80% correct classification in the crossvalidation analysis (table 5.5). Additionally, as with the South Asians, a strong regional morphology is evident in the Southeast Asian samples of this study (figures 5.3 and 5.4). This finding appears to be in contrast to previous research that has found a more diverse morphology for the region (Bowles, 1977; Lahr, 1996). The heterogeneity of the Southeast Asian samples in this study is, however, demonstrated by the significant Mahalanobis' distances between the samples (table 5.4) and the large percentages of correct classification in the discriminant analysis with cross validation (table 5.5). Again, following the South Asian samples, morphological variation is found within Southeast Asia but when compared to surrounding regional morphologies the overall trend is one of regional similarity. Hypothesis $\mathbf{H_1}$ stated that the populations of Southeast Asia are not morphologically distinct in craniofacial shape from those of South Asia. The results of this chapter demonstrate the presence of general morphologies for both South and Southeast Asia and therefore $\mathbf{H_1}$ is refuted.

Debates over the population history of Southeast Asia and the origins of the present day inhabitants revolve around two main questions. The first is whether the indigenous inhabitants of the region shared any affinity with populations from Australia and Melanesia. The second question regards the scale of dispersal from North and East Asia and whether there was substantial admixing of the populations within Southeast Asia. Studies of dentition (Turner, 1990, 1992) have proposed a shared ancestral history for Southeast Asians and Australian Aborigines. In addition, prehistoric Southeast Asian skeletons, such as the Moh Khiew and Niah cave specimens, have been compared with modern day Australian and Tasmanian morphologies (Matsumura, 2006; Brothwell, 1960). The second hypothesis, $\mathbf{H_2}$, set out to compare the samples from Island Southeast Asia with those from Melanesia and Australia to see if any affinity, as suggested by these arguments, is reflected in the present day populations. The analyses produced more complex results than those between the South and Southeast Asian samples. Some similarity in craniofacial shape between the Southeast Asians and the samples from New Guinea and the

Solomon Islands, was suggested by the analysis of all individuals (figure 5.8). The New Britain and New Caledonian samples, however, were placed together on a separate bifurcation of the phenogram (figure 5.8) as were the three Australian samples, demonstrating distinct morphologies for these groups. When the sample means were analysed with the inclusion of a greater number of Southeast Asian samples, however, the Southeast Asian samples appear more clearly distinct (figure 5.9). These findings again demonstrate the general regional morphology present in the Southeast Asians in relation to their neighbouring populations. This suggests a more complex demographic history between these regions than a simple shared ancestral history between Southeast Asians and the samples from Australia and Melanesia. No obvious continuity can be determined from the results, rather a complex pattern of morphological similarities and differences. The pattern of diversity may reflect an intricate history of migrations and population movements. The second null hypothesis, $\mathbf{H_2}$, that the populations of Southeast Asia are not morphologically distinct in craniofacial shape from those of Melanesia and Australia, is refuted. Some morphological similarity is observed, however, between certain samples from the regions.

Of the competing models for the origins of the modern Southeast Asians, that of immigration or local evolution, both could receive support from the results of the present study. The craniofacial similarities between the Southeast Asian samples and those from New Guinea and the Solomon Islands could be explained by the immigration model, in which migrants from East Asia occupied the region (Bellwood, 1997). Admixture with the East Asian migrants could account for the creation of the Southeast Asian regional morphology, and to a lesser extent in the New Guinean samples that share these craniofacial similarities, with a clinal distribution of the morphology eastwards. The Melanesian and Australian samples which are morphologically distinct may not have experienced admixture or only to a much reduced degree. The second model proposes that the modern Southeast Asian phenotype derived from local evolution and adaptation (Hanihara, 1994). The patterns of craniofacial diversity found in this chapter could also be accounted for by this scenario. As the results of Chapter 4 have shown, climatic factors can determine morphological variability to an extent. The regional clustering of the Southeast Asian samples, under the local evolution model, could be the result of adaptation to

similar environments. Any similarities with the neighbouring New Guinean samples could be due to a shared common ancestry and local admixture between the regions. This scenario is less likely, however, given that Southeast Asia is known to have a heterogeneous geography and therefore it is unlikely that the various populations adapted to similar environments. It is not possible, however, to test these two assertions fully with the samples available in the present study. To further explore the question of the development of the present day Southeast Asians it would be necessary to include pre-Neolithic samples from Southeast Asia and early samples from Melanesia and Australia. Morphological variation could therefore be assessed both in terms of time and space. Further exploration of these models would be of interest in future studies.

5.5.2 Morphological evidence for 'relic' populations

The Veddah of Sri Lanka, the Andaman and Nicobar Islanders are among groups that have been cited as possible 'relic' populations from the first migration around the Indian Ocean rim (Bellwood, 1997). The second section of this chapter explored whether any evidence of the 'relic' nature of these groups could be found in the cranial morphology. As 'relics' of the first migration out of Africa, it would be expected that these populations would retain some morphological similarity with populations from Africa. From the analyses including two African samples (section 5.4.1), it is clear that there is little craniofacial similarity between the proposed relic samples and the African samples, as the Africans are distinct from all of the South and Southeast Asian samples (table 5.4; figure 5.3). Although superficially likened to African populations (Dobson, 1875), there is no craniofacial similarity with the proposed relic groups. This finding supports the evidence from genetics that the Andaman Islanders and Nicobar Islanders demonstrate closer affinities with Asian rather than African groups (Endicott *et al.*, 2003a, b; Prasad *et al*, 2001).

Geographically the Andaman Islands are today part of India, however, in the analyses of the South Asian group they were clearly distinct from all other samples from that region (figures 5.3 and 5.4). The morphological distinctiveness of the Andaman Islanders is shown in the crossvalidation analysis where over 91% of individuals were correctly placed in their original group and they were situated as an outlier of the South Asians in the phenogram (table 5.5; figure 5.3). The Nicobar

Islands sample is also shown to be morphologically distinct. In the crossvalidation analysis (table 5.5) the Nicobar Islands sample achieves over 92% of correct classification and is placed as an outlier of all South and Southeast Asian samples on the phenogram (figure 5.3). In the analysis of the sample means, the Nicobar and Andaman Islanders can also be seen to be outliers from both the South and Southeast Asian clusters (figure 5.4). The combined shape of the Andaman and Nicobar Islands samples explains the morphological variation along PC2 (figure 5.4). This PC, which accounts for approximately 11.8% of the total sample variance, is associated mainly with changes in the lower facial region (figure 5.6). The results have demonstrated, therefore, that both the Andaman and the Nicobar Islanders are craniofacially distinct, both from each other and from the remaining South and Southeast Asian samples. Hypotheses $\mathbf{H_3}$ and $\mathbf{H_4}$, that the craniofacial skeletons of the Andaman and Nicobar Islands are not morphologically different from those of other South or Southeast Asian populations, are therefore both refuted.

In contrast to the Nicobar and Andaman Islanders, the Veddah do not show marked differences from the other samples from South Asia. Within the South Asian analyses, misclassified Veddah specimens are spread amongst the other Sri Lankan and mainland Indian samples, with none attributed to the Andaman or Nicobar samples (table 5.5). Similarly, the Mahalanobis' distances between the Veddah and the South Asian samples are smaller than those between the Veddah and the Andaman and Nicobar samples (table 5.4). In the PCA of the sample means (figure 5.4) the Veddah are situated within the general South Asian cluster rather than as an outlier with the other proposed 'relic' samples. On the phenogram produced from the Mahalanobis' distances, the Veddah are situated in the same cluster but as the outmost branch, of the other mainland India and Sri Lankan samples (figure 5.3). There is an obvious difference between the distinctiveness of the Andaman and Nicobar Island samples and the homogeneity of the Veddah as part of the general South Asian morphology (figure 5.3). Based on the craniofacial skeleton of the supposed 'relic' populations, it is therefore clear that whilst the Andaman and Nicobar Islanders are outliers from the South and Southeast Asian samples, the Veddah are representatives of the South Asian regional morphology. In contrast to the Andaman and Nicobar Islands samples, therefore, the Veddah are not significantly different from the other South Asian samples and thus $\mathbf{H_5}$ is not refuted.

Linguistic evidence suggests that the Veddah have been admixed with the Singhalese for a considerable amount of time (Kennedy, 2003) and this appears to be reflected in the cranial morphology. Although it is not possible to state whether the original inhabitants of Sri Lanka were part of the first wave of migration out of Africa (Deraniyagala, 1992) it can be stated that the Veddah, as represented by the samples in this study, do not appear to be a 'relic' population.

In terms of the craniofacial skeleton, the Nicobar and Andaman Islanders are more likely candidates for 'relic' status as they are so morphologically distinctive from other South and Southeast Asians. It is demonstrated, however, that no homogenous 'relic' morphology can be identified from the proposed representative populations within this study. As well as being distinct from the South and Southeast Asian samples, both the Andaman and Nicobar samples are additionally distinct from one another. Whilst the Nicobar and Andaman Islanders are identified as being craniofacially dissimilar to their regional counterparts, this does not confirm their status as 'relic' populations from the original migration out of Africa. Genetically and linguistically the Nicobarese are linked to Southeast Asian populations, with a suggested split about 18,000 years ago (Thangaraj *et al.*, 2005). Linguistic and some molecular evidence may provide a greater claim for the Andaman Islanders being a 'relic' population than for the Nicobarese, including the Indo-Pacific languages and the genetic data suggesting an isolation period of up to 60,000 years (Endicott *et al.*, 2003a; Thangaraj *et al.*, 2005). More recent molecular evidence, however, demonstrates that the Andaman Islanders were probably not part of the original wave of settlement out of Africa, with related genomes being found within populations from mainland India (Palanichamy *et al.*, 2006; Thangaraj *et al.*, 2006). The combined evidence does not, therefore, support the claims that the Nicobar and Andaman Islanders are relics of the first migration out of Africa.

The morphological distinctiveness of the Nicobar and Andaman Islanders must therefore be determined by something other than their being ancestors of the pioneer migrants out of Africa. As shown in the previous chapter, differences in craniofacial morphology can develop through a complex range of processes including founder effect, genetic drift and adaptation to differing environments. The small population sizes of these two groups, along with the small range of islands they inhabit must

have played a part in creating the distinctive morphology found today. It is known that dramatic evolutionary changes can occur in species that are isolated on islands (Millien, 2006). The Andaman Islanders have been isolated for a long period and are notoriously protective of their isolation, meaning that founder effect could have been instrumental in creating their discrete morphology. The Nicobar Islands have had much more contact with mainland Southeast Asia and therefore the role of repeated founder effects on a small population could have been important.

5.5.3 Summary of craniofacial shape variation within South and Southeast Asia

This chapter has assessed the morphological distinctiveness of extant South and Southeast Asians. Traces of the original Late Pleistocene dispersal are not clearly identifiable from the South and Southeast Asian samples included in this study. Regional morphologies remain the main aspect of the patterns of craniofacial variation found within these areas. Later migrations and population movements, combined with factors such as genetic drift and adaptation to local environments have obscured any morphological evidence of the Late Pleistocene dispersal in present day populations. In this chapter it has also been demonstrated that there is no morphological evidence for populations being 'relics' of this original migration. The Veddah, the Andaman and Nicobar Islanders do not share a common craniofacial shape and it is unlikely that they represent the morphology of the first migrants from Africa. Whilst there is an observable morphological discontinuity of certain isolated populations such as the the Andaman and Nicobar Islanders, this distinction is likely to have been caused by the combined effects of isolation, founder effect, genetic drift and adaptation to differing environmental conditions. Similar morphological distinctions in isolated populations such as the Ainu were identified by Hanihara (2003).

- There is suggestion of a South Asian cranial morphology, although diversity is present throughout the subcontinent

- South Asian diversity is suggested to be primarily due to a long period of occupation rather than from the numerous migrations into the sub-continent

- The presence of a general Southeast Asian cranial morphology is found, in contrast to a heterogeneous nature as described by previous research

- There is no clear evidence to accept or reject the two main models presented for the evolution of the modern Southeast Asian phenotype, though some support is given for the immigration model due to differing environments found within the region

- There is no craniofacial evidence that the Veddah and the inhabitants of the Andaman Islands and Nicobar Islands are 'relics' of the Late Pleistocene dispersal out of Africa.

Chapter 6

Craniofacial Diversity in Melanesia and Australia

6.1 Introduction

This chapter deals with the second major regional clustering identified in Chapter 3, that of Melanesia and Australia. The proposed Late Pleistocene dispersal from Africa progressed along an eastwards route through South and Southeast Asia, finally terminating in Melanesia and Australia. No further migration occurred in these terminal locations until during the Holocene. After the initial settlement of the Sahul continent, Melanesia and Australia subsequently followed different paths in terms of migration and dispersal. The chapter is therefore split into two sections, firstly concentrating on Melanesia alone and secondly looking at Australian morphology and comparing it with that found in Melanesia.

6.1.1 Craniofacial diversity in Melanesia

One of the known terminal points of the Late Pleistocene dispersal from Africa was situated in Melanesia. The north-westerly islands of Melanesia, including New Guinea, New Britain, New Ireland and the Solomon Islands (figure 6.1) were first colonised from approximately 45,000 BP (O'Connell and Allen, 2004). Colonisation of the remainder of Melanesia, to the east of the Solomon Islands, did not occur until approximately 3,500 BP. One of the earliest sites in Melanesia dates to approximately 40,000 BP and is situated on the Huon Peninsula of northern New Guinea (Groube *et al.*, 1986). An early settlement date is also given for the site of Buang Merabak on New Ireland, first occupied at around 39,500 BP (Leavesley *et al.*, 2002).

Geographically, the islands and archipelagos of Melanesia have a fairly isolated position, situated adjacent to New Guinea at their northern end (figure 6.1). The islands of Melanesia have never been physically attached to one another and remained geographically isolated even during the periods of low sea level during the Late Pleistocene when New Guinea, Australia and Tasmania were joined as the Sahul continent. Melanesia extends from approximately 2 degrees south of the

Equator, to New Caledonia at 22 degrees south, and the entire range of tropical latitudes is covered (Spriggs, 1997). The islands of Melanesia therefore show disparate environmental conditions. Little seasonality in rainfall or temperature is evident in the more northerly islands near the equator. Towards the southern islands of Vanuatu and New Caledonia, however, seasonality is quite marked, with distinctive wet and dry seasons (Spriggs, 1997).

A major biological distinction exists between New Guinea and the remainder of Island Melanesia, with a much greater level of diversity in plant and animal species found in mainland New Guinea than on the islands (Green, 1991). A further biological distinction exists between the islands of what Green (1991) has termed 'Near' and 'Remote' Oceania (figure 6.2). Near Oceania includes New Guinea, the Bismarck Archipelago and the islands of the Solomon's chain, and Remote Oceania consists geographically of all the Pacific islands to the north, east and southeast of Near Oceania (figure 6.2). Near Oceania has the greatest biogeographic diversity within Oceania (Kirch, 2000) and thirty genera of land birds and over 150 genera of seed plants have their eastern limits at the Solomon's chain. Beyond these islands there are no terrestrial mammals which have not been transported by human means (Spriggs, 1997). Both Austronesian and Papuan languages are spoken by the peoples of Near Oceania (Foley, 1986). Archaeological evidence suggests that the migration of *Homo sapiens* did not occur beyond the Solomon Islands during the initial colonisation (Bellwood, 1997). Remote Oceania, in contrast, contains much less biogeographic diversity than Near Oceania and the inhabitants speak exclusively Austronesian languages (Kirch, 2000).

Inferences for the dispersal of modern humans across Island Melanesia are made implicit with the artificial split into Near and Remote Oceania (Green, 1991). The boundary between the two areas serves as the known boundary between those settled during the Late Pleistocene and those not settled until the later Lapita cultural complex expansion, dating to approximately 3,500 BP (Spriggs, 1997). Although much of the Solomon's chain was at times joined as a single island, it did not extend any further north towards New Ireland than the existing islands do today. The evidence of early occupation suggests relatively low population numbers, living in dispersed coastal settlements (Gosden, 1993). These low population levels and the

poverty of natural resources in the area, suggests that the early migrant groups were not biologically or socially self sufficient (Gosden, 1993). Evidence exists of contact between islands from around 20,000 BP, with flakes of obsidian from New Britain appearing in New Ireland (Spriggs, 1997). There is no evidence at present of large scale immigration into Melanesia after the first early settlers. The next important migratory event is the influx of the Lapita cultural complex, around 3,500 BP, possibly from a Southeast Asian source (see also Chapter 7) (Bellwood, 1997).

The current inhabitants of Melanesia demonstrate extreme diversity in terms of language, culture and biology. Kirch (2000) describes Melanesia as having no cultural or historical unity, reflecting the long and complex history of migration into the region. The biological variation is so great that Howells (1970) stated that the Melanesians resisted satisfactory analysis. Molecular variation, however, indicates some correlation between certain genetic markers and populations distinguished as either Austronesian or Papuan speakers (Merriwether *et al.*, 1999, 2005). Friedlaender (1987) suggests that patterns of genetic and linguistic variation found in island Melanesia are often reflections, to varying degrees, of the migratory history of the region. Thus, although heterogeneous in terms of language, culture and biological variation, certain underlying patterns may be discerned in Melanesia which reflect a deep and complex history for this part of the world. Of all Melanesia, Near Oceania proves to be the most genetically and linguistically diverse sector, an observation with considerable historical significance, since diversity frequently implies great time depth (Robledo *et al.*, 2003).

Hypotheses

This chapter will explore the patterns of craniofacial diversity found in extant populations of Melanesia. Its aim is to elucidate whether the migratory history of the peoples of Melanesia can be determined from the current phenotypic differences in the craniofacial skeleton. Firstly, the chapter will assess whether the above mentioned genetic and linguistic diversity is reflected in the craniofacial morphology of the extant populations. This will be done by analysing whether the inhabitants of the diverse islands of Melanesia can be distinguished morphologically from another and thus the following null hypothesis is erected:

H_1 "The geographically distinct populations of Melanesia are not morphologically distinct in craniofacial shape from one another"

The hypothesis will be refuted if statistically significant differences between the disparate Melanesian samples are found. If the hypothesis is refuted then the patterns of craniofacial diversity within Melanesia will be further explored in relation to the proposed migratory events into the region. The distinction between Near and Remote Oceania is not merely a geographic division, but one that reflects two major epochs in the population history of Melanesia (Kirch, 2000). The restriction of Papuan languages within the Pleistocene settled Near Oceania and the distribution of Austronesian languages throughout Holocene settled Remote Oceania suggest the possibility that colonisation of these regions was undertaken by distinct populations. A second hypothesis will therefore explore whether there is a distinction in craniofacial morphology between the inhabitants of Near and Remote Oceania. The following null hypothesis is erected:

H_2 "The populations of the islands of Near Oceania are not morphologically distinct in craniofacial shape from those of Remote Oceania"

This hypothesis will be refuted if there are statistically significant differences between the samples from Near Oceania and those from Remote Oceania.

6.1.2 Craniofacial diversity in Australia

Like Melanesia, Australia is another terminal point of the original migration of *Homo sapiens* out of Africa. Australia was first settled by at least 45,000 BP (O'Connell and Allen, 2004), though some researchers prefer an earlier date of around 65,000 BP (O'Connor and Chappell, 2002). Given the earliest settlement dates for both Melanesia and Australia, it is possible that they were settled as part of this same, early population movement. Allen (2003) proposes that there were two contemporaneous settlement routes taken, one to Australia and the other leading to New Guinea and Island Melanesia. At this time, however, lower sea levels meant that Australia and New Guinea were joined along the Torres Strait Bridge (Webb, 2006).

Two main competing colonisation scenarios for the Pleistocene occupation of Australia exist (Bowdler, 1993; Flannery, 1994; O'Connell and Allen, 1998; Pardoe, 2006). These models in part are determined by the variable morphology of Australian fossil skeletons dating from the Pleistocene to the Holocene. The Australian fossils show considerable diversity in morphology, which has been interpreted by some researchers as reflecting two distinct populations (Thorne, 1976). A morphologically gracile population is seen in the Lake Mungo remains, in particular LM3, which has been dated to around 60,000 years old, though these dates have been heavily contested (Thorne *et al.*, 1999; Bowler *et al.*, 2003). The second population is purportedly represented by the Kow Swamp skeletons, which demonstrate a more robust morphology and date to the end of the Pleistocene (Stone and Cupper, 2003). The oldest and most consistent model of Australian origins is one that emphasises the unitary origin of Aboriginal people (Pardoe, 2006). Under this model, much of the biological variation is the result of change within Australia, with all Aboriginal people deriving from an early founding population along the north coast of the country. This model would allow for heterogeneous mtDNA lineages in the founding population and is primarily an evolutionary model that accounts for the biological variation through adaptation and gene flow. Alternatively, the differences in morphology found within Australian Aborigines are accounted for by waves of migration into Australia (Birdsell, 1967; Tindale, 1974; Thorne, 1976). Birdsell (1967) and Tindale (1974) put forward a tri-hybrid model where three different colonisation groups moved into the continent and displaced earlier migrants further south. Under this model biological variation is accounted for by three separate founding populations. A similar di-hybrid model is suggested by Thorne (1976) in which he explicitly equates the gracile and robust fossils with early and late migratory populations respectively. Again, as with South and Southeast Asia, the question of the origins of Australians can be seen to be contentious and currently unresolved.

Linguistic and genetic data suggest there was little or no contact between Australia and Melanesia following their initial settlements. There are no linguistic connections between Aboriginal Australian and New Guinea-Island Melanesian languages and Australian languages are confined to Australia and the western Torres Strait Islands (Dixon, 1980). Evidence from mtDNA further suggests that Australia has undergone

a substantial period of isolation from New Guinea and Island Melanesia (Friedlaender *et al.*, 2005; Merriwether *et al.*, 2005). Two haplogroups, P and Q, have been identified as being specific to the general Southwest Pacific region (Friedlaender *et al.*, 2005; Merriwether *et al.*, 2005). Haplogroup Q, found only in New Guinea and Island Melanesia is absent from Australia (Merriwether *et al.*, 2005). Haplogroup P is more widespread and heterogeneous than Q and, with only one exception, different branches of P are found either in Australia or New Guinea, but not both (Merriwether *et al.*, 2005). The extremely localised distributions of specific haplotypes within the branches of Q and P are consistent with highly restricted female movement within the region following initial settlement (Friedlaender *et al.*, 2005). Similarly the distributions of haplotype M branches further suggest a distinction between Australian and Near Oceanian populations (Merriwether *et al.*, 2005). Generally a picture of internal and ancient diversity is produced by the Southwest Pacific mtDNA variants. The diversity is maintained by long term isolation across the entire region. Friedlaender *et al.* (2005) suggest that the first female members of Sahul might have effectively been members of the same population, but if this is the case they then split into two groups shortly afterward and remained effectively isolated thereafter.

Hypotheses

The overall aim of this chapter is to explore the craniofacial morphology of Melanesian and Australian samples in relation to the proposed southern migration during the Late Pleistocene. As discussed above, Australia and Melanesia may have been colonised by a shared ancestral population dispersing from Southeast Asia and therefore this chapter will assess the degree of morphological similarity and difference between these samples.

Additionally, the chapter will address the issue of the 'Australo-Melanesian' classification. Despite the linguistic and genetic evidence pointing to long term isolation between Australia and Melanesia, traditional craniometric studies have long used the combined classification 'Australo-Melanesian' (Howells, 1989; Bellwood, 1997; Pietrusewsky, 2006) for populations from these regions. This classification is not clearly defined and often used as a term for skeletal remains for both fossil remains from Southeast Asia and Oceania and also generally for referring to modern

populations particularly from Oceania (Howells, 1989; Bellwood, 1997). Even amongst those who use the term as a classification it is considered an idealised model (Bellwood, 1997) and therefore it is prudent to explore whether the linguistic and genetic separation between Australia and Melanesia is additionally reflected in the craniofacial morphology of the extant populations.

The following null hypothesis is erected:

H_3 "The populations of Melanesia are not morphologically distinct in craniofacial shape from Australian Aboriginal populations"

This hypothesis will be refuted if there are statistically significant differences between the Melanesian and Australian populations.

6.2 Materials

The materials in this study represent sub-sets of extant populations that are found in New Guinea, Island Melanesia and Australia. The samples consist of mixed sex specimens. Table 6.1 summarises the sample sizes for each population. Due to their small size, samples marked ** are used only in the analyses of sample means. Further details of the provenance of these specimens, assessment of maturation and determination of inclusion can be found in the materials section of Chapter 2.

Figure 6.1 Map of Island Southeast Asia, Melanesia and Australia

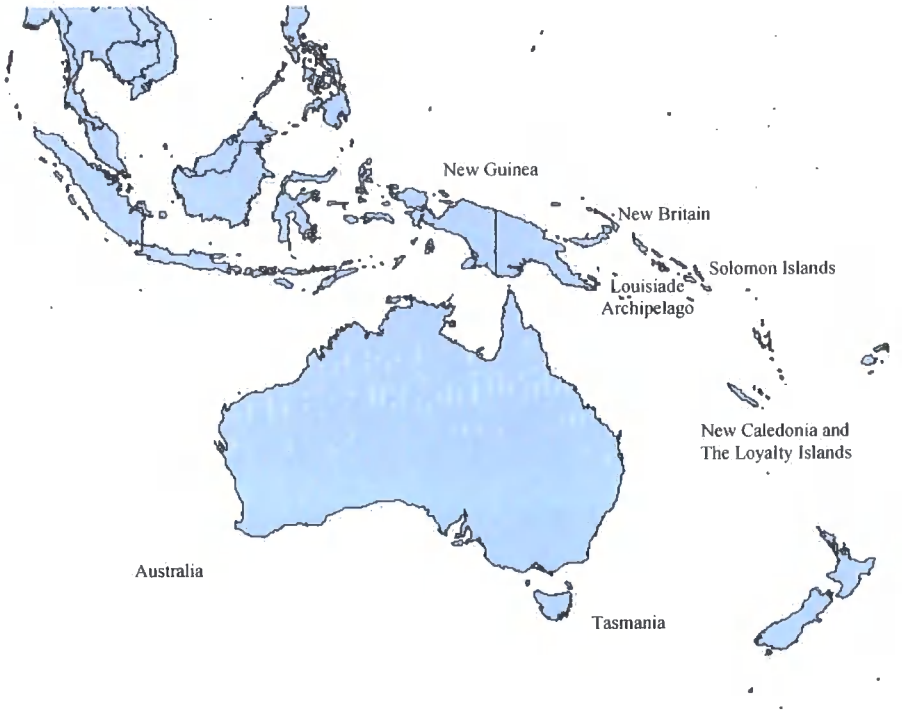
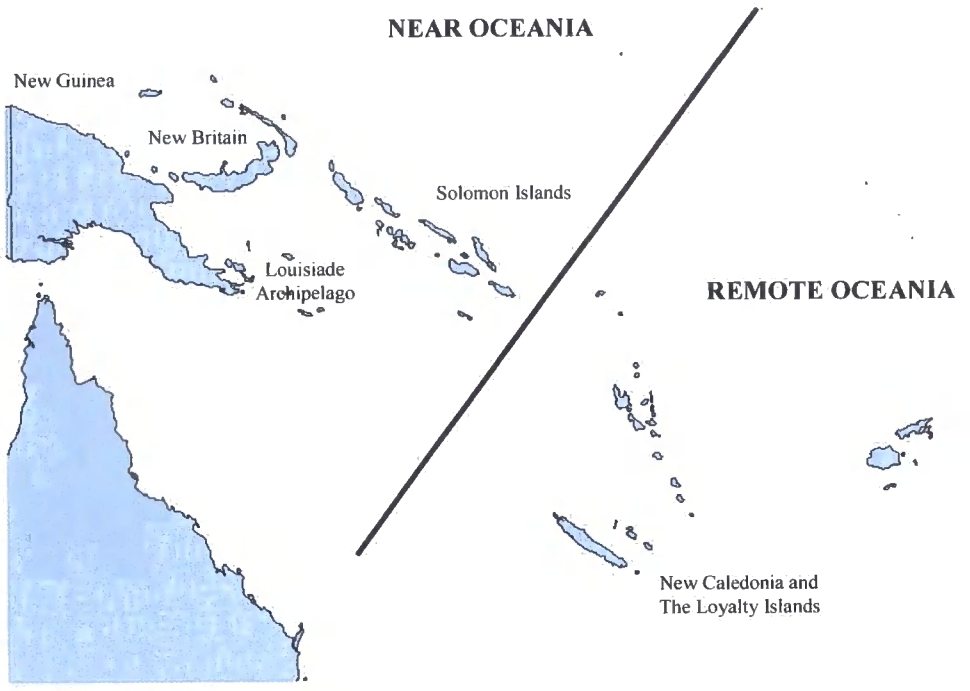


Figure 6.2 Map illustrating Near and Remote Oceania



6.3 Methods used in this chapter

Biological Distances

The degree of differentiation in shape between the groups is measured using Mahalanobis' D for the complete samples. Mahalanobis' D, or generalised distance, is a function of the group means and the pooled variances and covariances among populations. Mahalanobis' D is used to test whether group centroids are significantly different and the discriminatory power of that distance.

Discriminant Analysis

Discriminant analysis with crossvalidation is used to classify individuals into predefined groups, based upon Mahalanobis' D^2 distances. Each individual is assigned a probability of belonging to a given group based on the distance of its discriminant function from that of each group mean. Crossvalidation is employed as it provides a better assessment of classification accuracy than standard discriminant analysis. During crossvalidation, classification is carried out for each individual in turn and the discriminant function used in each case is constructed with that individual removed. The crossvalidation analyses are carried out using SAS (The SAS Institute Inc., 1996).

Distance Phenograms

Utilising the Mahalanobis distances, UPGMA phenograms were constructed in order to summarise the morphological relationships between the groups. The phenograms were created using the program NTSYS (Exeter Software).

Table 6.1. Melanesia and Australia: Composition of data sets

Region	Country	Sample	Sample Size	Specimen Location*
Melanesia				
	New Guinea	Awaiama	19	DC
	New Guinea	Kwaiawata	18	DC
	New Guinea	Sinaugolo	21	NHM, DC
	New Britain	New Britain	35	NHM, DC
	Solomon Islands	Solomon Islands	21	NHM, O, DC
	Louisiade Archipelago	Louisiade Archipelago**	10	NHM, O
	New Caledonia	New Caledonia	15	NHM, DC
	Loyalty Islands	Loyalty Islands**	7	NHM
Australia				
	Australia	New South Wales	24	NHM, O, DC
	Australia	South Australia	16	NHM, O, DC
	Australia	Tasmania	12	NHM, O
Total			**198**	

* NHM, Natural History Museum, London; O, The University Museum of Natural History, University of Oxford: DC, The Duckworth Laboratory, University of Cambridge.

** Used only in the analyses of sample means.

6.4 Results

6.4.1 Craniofacial diversity in Melanesia

Principal components analysis is conducted on the Procrustes fitted data from six geographically distinct Melanesian samples. The samples are the Awaiama, Kwaiawata and Sinaugolo from New Guinea, and New Britain, New Caledonia and Solomon Islands from Melanesia. Table 6.2 lists the principal components scores for the total sample variance. PC1 explains 10.8% of the total sample variance and PC2 7.7%. Some limited separation between the New Guinea (in blue) and Island Melanesian (in pink) samples can be observed along a combination of PCs 1 and 2, however there is still considerable overlap of the samples (figure 6.3). No further separation between samples can be identified on any other single PC.

Figure 6.3. Melanesia: PC 1 v PC 2

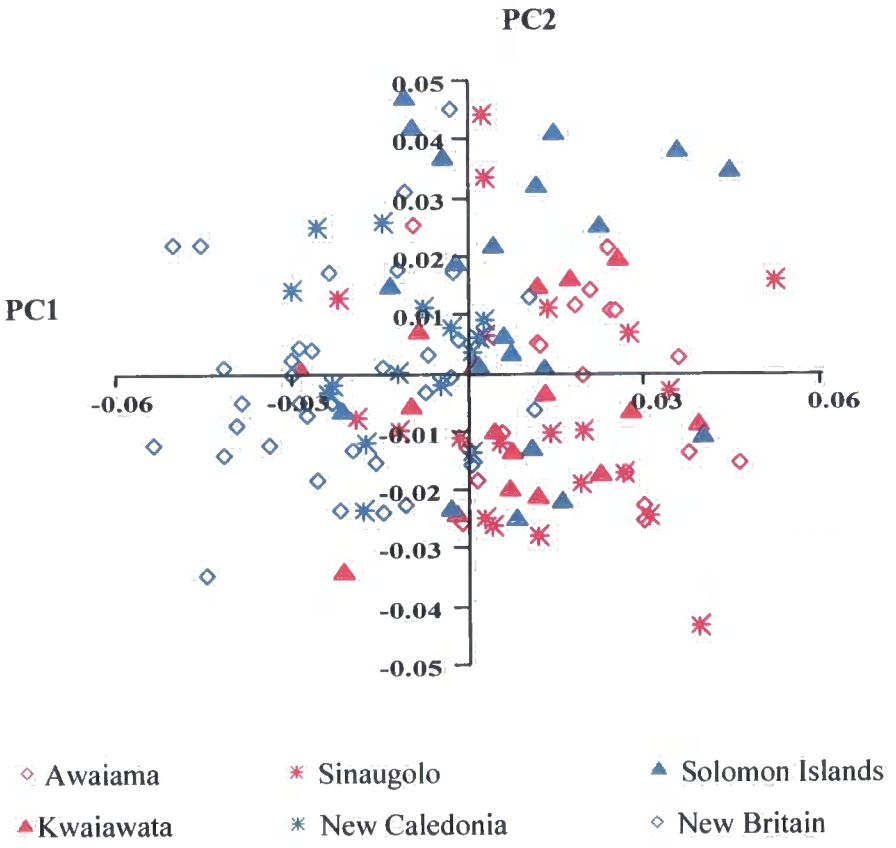


Table 6.2 Melanesia: The proportion of and accumulated variance of PCs 1 – 116, which account for almost 100% of total sample variance

PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %
1	10.80	10.80	**35**	0.68	85.49	**69**	0.15	97.42	**103**	0.02	99.79
2	7.73	18.53	**36**	0.65	86.14	**70**	0.15	97.57	**104**	0.02	99.81
3	6.86	25.39	**37**	0.64	86.78	**71**	0.14	97.71	**105**	0.02	99.83
4	5.97	31.36	**38**	0.58	87.36	**72**	0.14	97.84	**106**	0.02	99.85
5	4.63	35.99	**39**	0.56	87.92	**73**	0.13	97.97	**107**	0.01	99.86
6	4.20	40.19	**40**	0.55	88.47	**74**	0.12	98.09	**108**	0.01	99.88
7	3.89	44.08	**41**	0.53	89.00	**75**	0.11	98.20	**109**	0.01	99.89
8	3.59	47.67	**42**	0.52	89.52	**76**	0.10	98.31	**110**	0.01	99.90
9	2.88	50.55	**43**	0.50	90.02	**77**	0.10	98.40	**111**	0.01	99.91
10	2.83	53.38	**44**	0.48	90.50	**78**	0.10	98.50	**112**	0.01	99.92
11	2.44	55.82	**45**	0.44	90.94	**79**	0.09	98.59	**113**	0.01	99.93
12	2.35	58.17	**46**	0.43	91.37	**80**	0.09	98.68	**114**	0.01	99.93
13	2.06	60.23	**47**	0.41	91.78	**81**	0.08	98.76	**115**	0.01	99.94
14	1.86	62.09	**48**	0.39	92.17	**82**	0.08	98.84	**116**	0.01	99.94
15	1.83	63.92	**49**	0.38	92.54	**83**	0.08	98.92			
16	1.77	65.69	**50**	0.35	92.89	**84**	0.07	98.99			
17	1.57	67.26	**51**	0.34	93.23	**85**	0.07	99.07			
18	1.46	68.72	**52**	0.33	93.56	**86**	0.07	99.14			
19	1.43	70.15	**53**	0.31	93.87	**87**	0.06	99.20			
20	1.36	71.51	**54**	0.30	94.18	**88**	0.06	99.26			
21	1.30	72.81	**55**	0.29	94.46	**89**	0.05	99.31			
22	1.23	74.04	**56**	0.28	94.74	**90**	0.05	99.36			
23	1.15	75.19	**57**	0.27	95.01	**91**	0.05	99.41			
24	1.12	76.31	**58**	0.25	95.26	**92**	0.05	99.46			
25	1.04	77.35	**59**	0.25	95.51	**93**	0.04	99.50			
26	0.98	78.33	**60**	0.24	95.74	**94**	0.04	99.54			
27	0.94	79.27	**61**	0.23	95.97	**95**	0.04	99.57			
28	0.90	80.17	**62**	0.21	96.18	**96**	0.03	99.61			
29	0.83	81.00	**63**	0.20	96.38	**97**	0.03	99.64			
30	0.82	81.82	**64**	0.19	96.57	**98**	0.03	99.67			
31	0.79	82.61	**65**	0.19	96.76	**99**	0.03	99.70			
32	0.77	83.38	**66**	0.17	96.93	**100**	0.03	99.72			
33	0.72	84.10	**67**	0.17	97.10	**101**	0.02	99.75			
34	0.71	84.81	**68**	0.16	97.26	**102**	0.02	99.77			

To assess the effects of noise factors in the analyses such as intra-population variation, separate discriminant analyses using differing amounts of variance are performed on the data (table 6.3). The rationale of this method is outlined in Chapter 3. Using approximately 80% of the total variance produces the optimal level of discrimination between samples and the subsequent analyses for the Melanesian samples are performed using PCs 1-28.

Table 6.3 Melanesia: Cross validation study to assess the separation by proportion of sample variance

Sample	70% (PCs 1-19)	80% (PCs 1-28)	90% (PCs 1-43)	95% (PCs 1-57)	100% (PCs 1-116)
ANG	57.89	63.16	63.16	68.42	0.00
KNG	61.11	61.11	38.89	44.44	0.00
SNG	38.10	42.86	52.38	57.14	0.00
NB	74.29	77.14	80.00	71.73	100.00
SI	71.43	71.43	57.14	66.67	0.00
NC	40.00	46.67	46.67	53.33	0.00
Mean	**57.14**	**60.40**	**56.37**	**60.29**	**16.67**

The Mahalanobis' distances between the samples are given in table 6.4. All distances are statistically significant ($p \leq 0.05$), demonstrating that there are significant differences in some aspect of craniofacial shape between all six populations. The smallest distance is found between the Solomon Island sample and the Sinaugolo sample from New Guinea (D = 7.32) and the largest between the New Britain sample and the Awaiama from New Guinea (D = 23.10).

The results of the cross validation analysis of the Melanesian samples are given in table 6.5. Overall, 60.4% of the individuals are correctly classified to their original sample. The sample with the highest percentage of correct classification is from New Britain (77.14%). The Sinaugolo sample, from New Guinea, has the least number of individuals correctly classified (42.86%), with a large number of misclassified individuals being placed in the Awaiama and Solomon Island samples. The misclassified individuals from the Awaiama and Kwaiawata samples are generally placed within alternate New Guinea samples. The New Caledonian sample has a relatively high number of misclassified individuals placed in the Kwaiawata

and Sinaugolo samples from New Guinea. There is no statistical correlation between the number of individuals in each sample and the percentage of correct classification in this analysis.

Table 6.4 Mahalanobis' D distance matrix: Melanesia; * significant at $p \leq 0.05$
ANG, Awaiawama (New Guinea); KNG, Kwaiawama (New Guinea); SNG, Sinaugolo (New Guinea); NB, New Britain; SI, Solomon Islands; NC, New Caledonia.

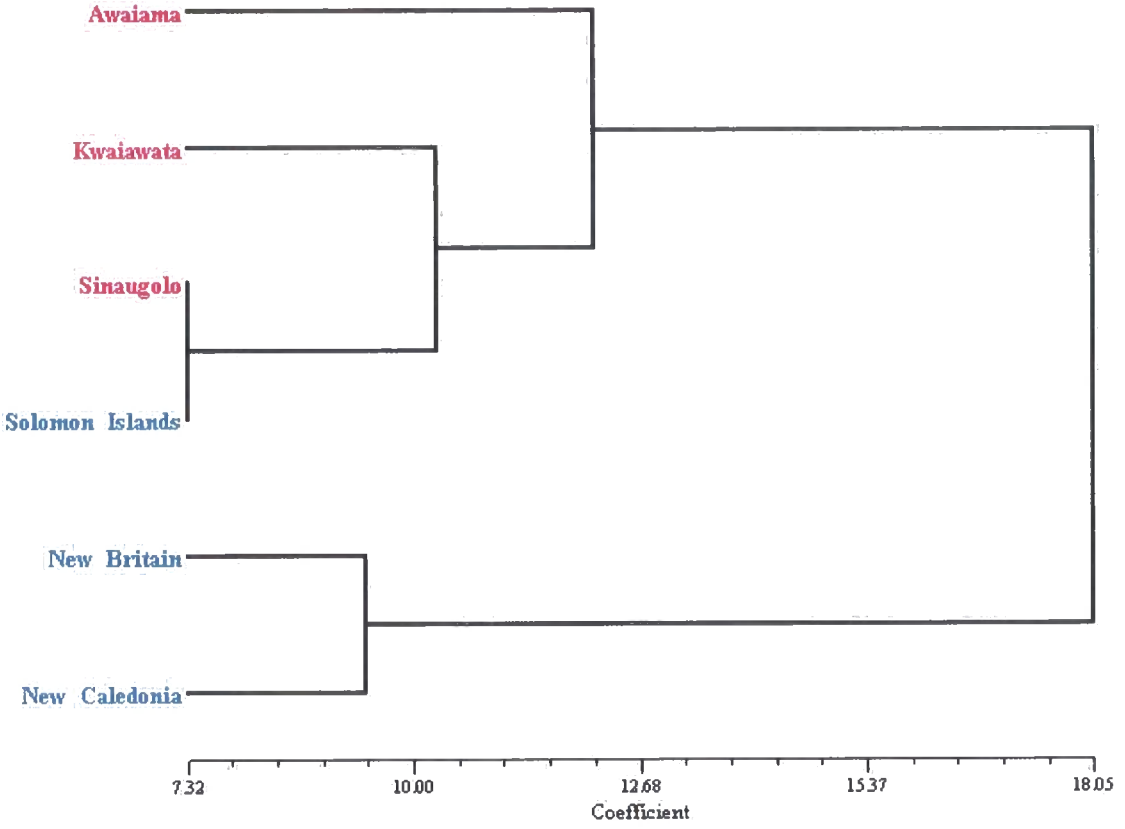
	ANG	KNG	SNG	NB	SI	NC
ANG	0.00					
KNG	12.85*	0.00				
SNG	9.21*	9.49*	0.00			
NB	23.10*	18.17*	16.66*	0.00		
SI	14.34*	11.04*	7.32*	15.97*	0.00	
NC	18.63*	14.17*	16.41*	9.44*	21.29*	0.00

Table 6.5 Cross validation analysis: Melanesia
ANG, Awaiawama (New Guinea); KNG, Kwaiawata (New Guinea); SNG, Sinaugolo (New Guinea); NB, New Britain; SI, Solomon Islands; NC, New Caledonia.

	ANG	**KNG**	**SNG**	**NB**	**SI**	**NC**	**Total**
ANG %	**63.16**	10.53	15.79	5.26	0.00	5.26	100.00
KNG %	5.56	**61.11**	16.67	0.00	11.11	5.56	100.00
SNG %	19.05	9.52	**42.86**	0.00	23.81	4.76	100.00
NB %	0.00	0.00	2.86	**77.14**	5.71	14.29	100.00
SI %	4.76	14.29	4.76	4.76	**71.43**	0.00	100.00
NC %	0.00	26.67	13.33	6.67	6.67	**46.67**	100.00

A phenogram showing a two-dimensional representation of the morphological relationships between the samples based on the Mahalanobis' distances is given in figure 6.4. Two main branches are identifiable, with the New Britain and New Caledonian samples situated on the first bifurcation and the remaining samples on the other. On the second bifurcation, the Solomon Islands sample clusters with the three New Guinea samples.

Figure 6.4 Phenogram showing relative shape relationships between the Melanesian samples.



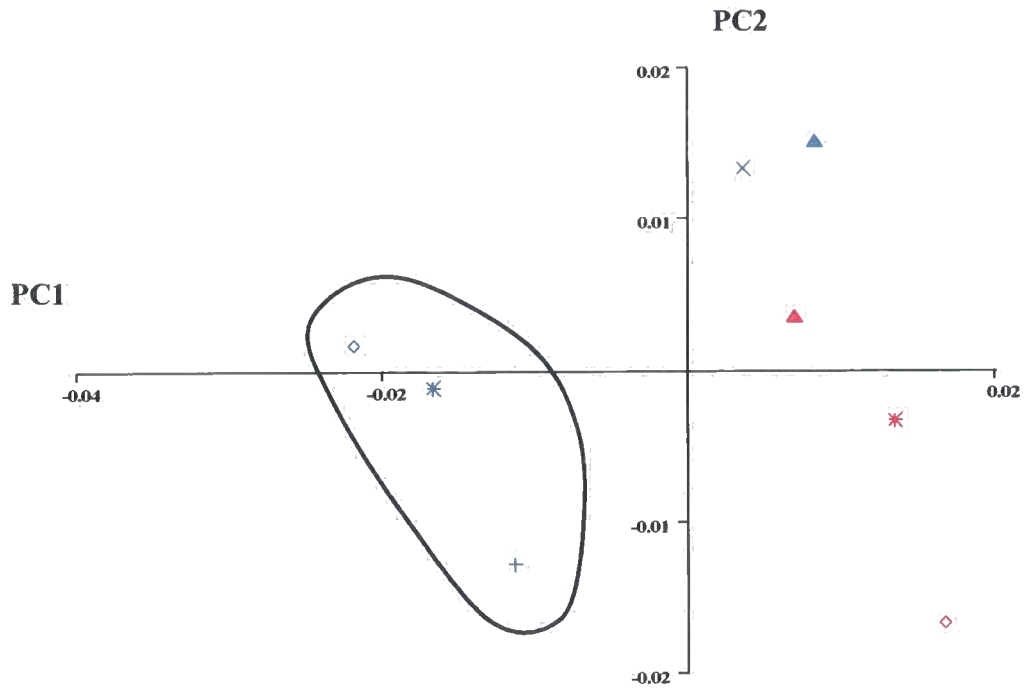
6.4.1a Craniofacial diversity in Melanesia: Means

Sample means are used to further explore the craniofacial diversity found in Melanesia and to allow the addition of samples too small to be included in the full data set analysis. The additional samples included are from the Louisiade Archipelago in Near Oceania and the Loyalty Islands in Remote Oceania. Each sample is subject to a separate GPA to calculate a sample mean and then a joint GPA and PCA are performed. Table 6.6 lists the amount of variance accounted for by each PC and figure 6.5 illustrates the results of the PCA for PC1 versus PC2. PC1 accounts for 31.7% of the total sample variance whilst PC2 explains a further 18.5%. No clear separation of the Near and Remote Oceanic samples is observed on either PC1 or PC2 and no other single PC separates the sample populations.

Table 6.6 Melanesia sample means: The proportion and accumulated variance of PCs 1 – 7, which account for 100% of total sample variance

Principal Component	Variance %	Cumulative Variance %
1	31.7	31.7
2	18.5	50.2
3	16.4	66.6
4	11.2	77.8
5	8.1	85.9
6	7.7	93.6
7	6.4	100.0

Figure 6.5. Near and Remote Oceania: PC 1 v PC 2



The New Britain, New Caledonian and Loyalty Islands samples (circled) are separated from the remaining samples along PC1 (figure 6.5). The mean shape configurations at the negative and positive extremes of PC1 are shown in figure 6.6, reflecting the differences in morphology between the circled cluster and the remaining samples. At the negative extreme of PC1 the morphology is characterised by extreme maxillary prognathism (figure 6.6 i) associated with a relatively posterior sloping face (figure 6.6 ii). The shape at the positive extreme is less prognathic, with the maxilla tucked beneath the nasal aperture (figure 6.6 iii). The upper face, between the nasal aperture and glabella is relatively more straight and anteriorly positioned at the positive extreme (figure 6.6 iv). The basicranium is also relatively decreased in length towards the positive extreme of PC1 (figure 6.6 v). Figure 6.7 illustrates the mean shape configuration at the negative and positive extremes of PC2. PC2 has much less observable morphological difference. Towards the positive

extreme glabella is situated relatively more superiorly and posteriorly (figure 6.7 i), whilst bregma and stephanion are positioned relatively more inferiorly and anteriorly (figure 6.7 ii). There is also a slight relative displacement of the zygomatic arch (figure 6.7 iii).

Figure 6.6 PC1 TPS: Differences in shape along the first PC. The upper figure represents the mean landmark configuration warped along PC1 from the negative to the positive extreme

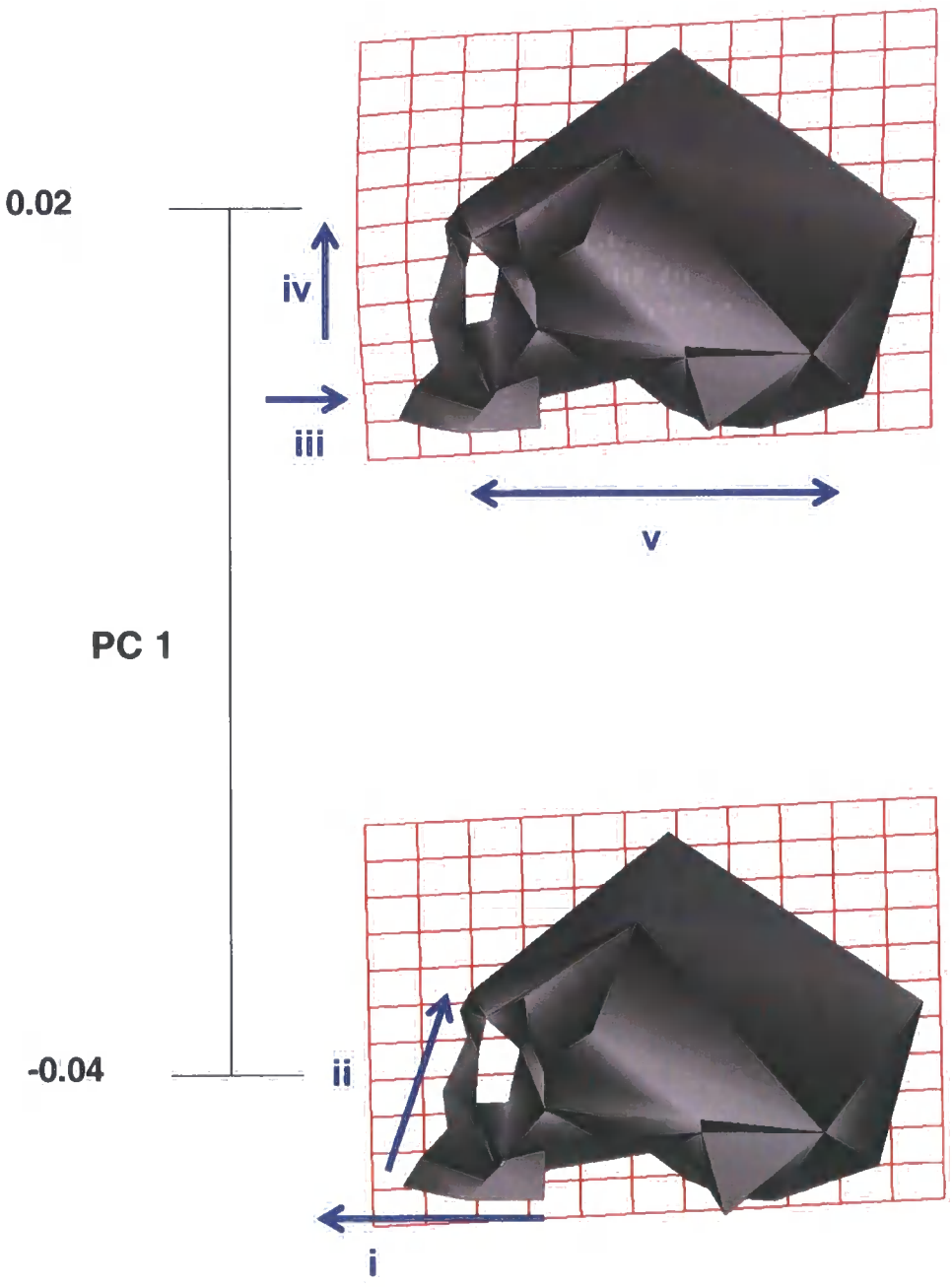
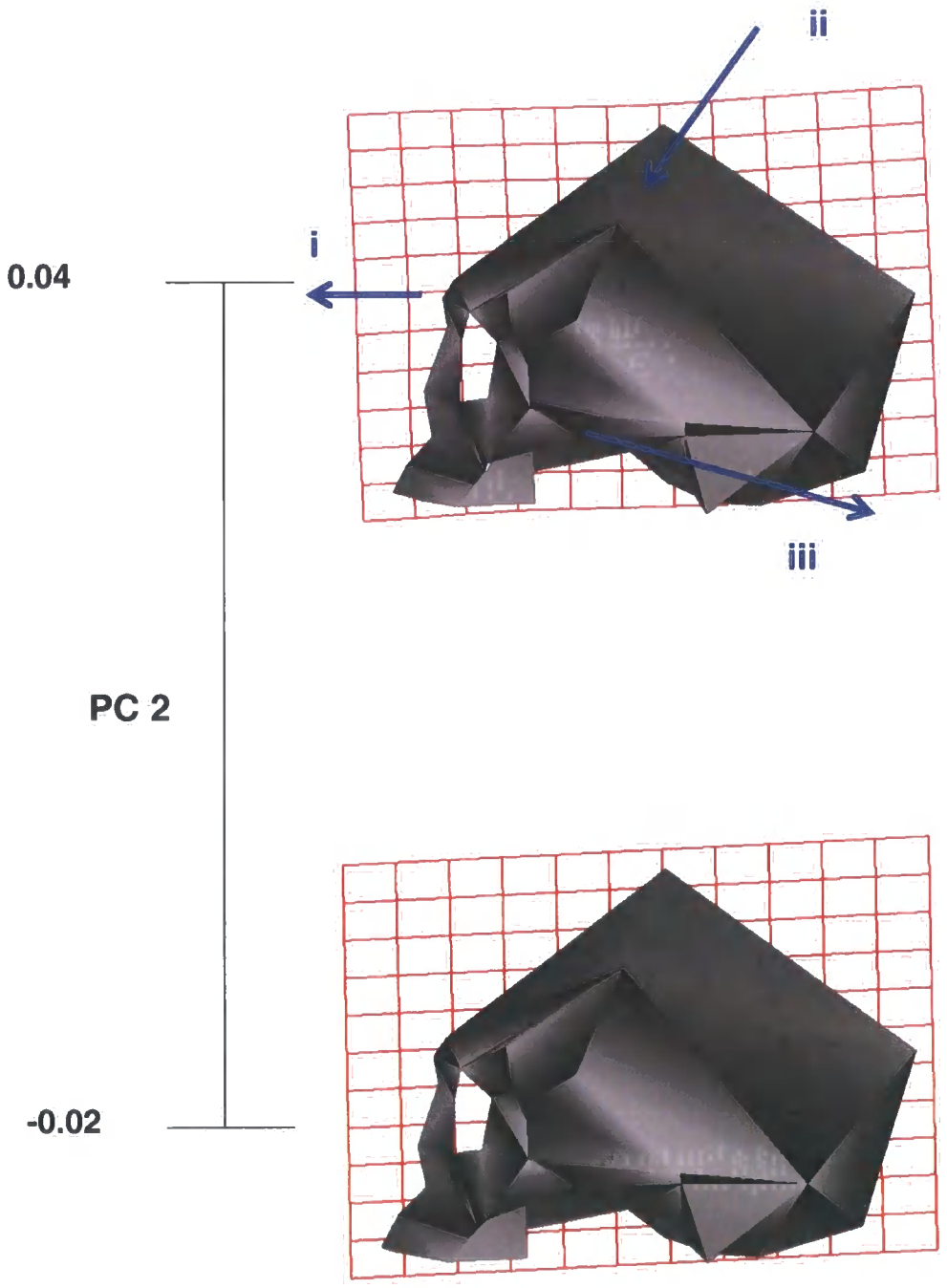


Figure 6.7 PC2 TPS: Differences in shape along the second PC. The upper figure represents the mean landmark configuration warped along PC2 from the negative to the positive extreme.



6.4.2 Craniofacial diversity in Melanesia and Australia

Having established that the populations of Melanesia are morphologically distinct from one another, three Aboriginal Australian samples are added to the analyses to explore the craniofacial shape relationships between these regions. Procrustes registration and principal components analysis is performed on the new data set using all individuals. The Australian samples are from New South Wales, South Australia and Tasmania. Table 6.7 lists the percentage of variance given by each PC. Alternate discriminant analyses are performed to test for optimal separation of samples and the following analyses are carried out using PCs1-31, explaining 80% of the total variance (table 6.8). PC1 versus PC2 is given in figure 6.8. No definable separation is found on PCs 1 or 2, or on any further single PC.

Figure 6.8. Melanesia and Australia: PC 1 v PC 2

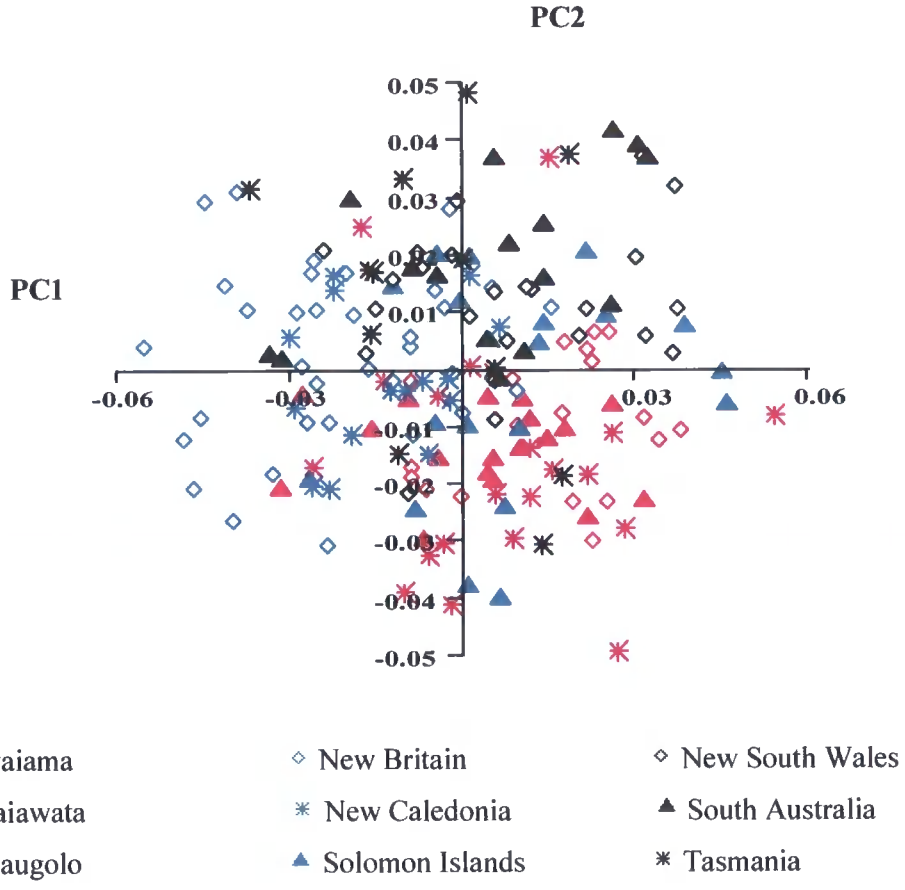


Table 6.7 Melanesia and Australia: The proportion of and accumulated variance of PCs 1 – 130, which account for 100% of total sample variance

PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %
1	9.64	9.64	**35**	0.68	83.21	**69**	0.19	96.03	**103**	0.04	99.45
2	7.61	17.25	**36**	0.66	83.88	**70**	0.18	96.21	**104**	0.04	99.49
3	6.71	23.96	**37**	0.63	84.50	**71**	0.18	96.38	**105**	0.04	99.53
4	5.89	29.85	**38**	0.62	85.13	**72**	0.17	96.55	**106**	0.04	99.56
5	4.45	34.30	**39**	0.60	85.73	**73**	0.16	96.71	**107**	0.03	99.60
6	4.19	38.49	**40**	0.59	86.31	**74**	0.16	96.86	**108**	0.03	99.63
7	3.84	42.33	**41**	0.54	86.85	**75**	0.15	97.01	**109**	0.03	99.66
8	3.29	45.62	**42**	0.52	87.37	**76**	0.14	97.16	**110**	0.03	99.69
9	2.96	48.58	**43**	0.50	87.87	**77**	0.14	97.30	**111**	0.03	99.72
10	2.73	51.31	**44**	0.48	88.35	**78**	0.14	97.43	**112**	0.02	99.74
11	2.49	53.80	**45**	0.46	88.81	**79**	0.14	97.57	**113**	0.02	99.77
12	2.31	56.11	**46**	0.46	89.28	**80**	0.13	97.70	**114**	0.02	99.79
13	2.09	58.20	**47**	0.45	89.72	**81**	0.12	97.82	**115**	0.02	99.81
14	1.91	60.11	**48**	0.42	90.15	**82**	0.11	97.93	**116**	0.02	99.83
15	1.82	61.93	**49**	0.41	90.56	**83**	0.11	98.04	**117**	0.02	99.85
16	1.70	63.63	**50**	0.39	90.95	**84**	0.11	98.15	**118**	0.02	99.87
17	1.58	65.21	**51**	0.37	91.32	**85**	0.10	98.25	**119**	0.02	99.88
18	1.41	66.62	**52**	0.35	91.67	**86**	0.10	98.35	**120**	0.01	99.90
19	1.40	68.02	**53**	0.34	92.01	**87**	0.09	98.45	**121**	0.01	99.91
20	1.37	69.39	**54**	0.33	92.34	**88**	0.09	98.54	**122**	0.01	99.92
21	1.27	70.66	**55**	0.31	92.65	**89**	0.09	98.63	**123**	0.01	99.94
22	1.26	71.92	**56**	0.31	92.96	**90**	0.08	98.71	**124**	0.01	99.95
23	1.19	73.11	**57**	0.30	93.25	**91**	0.08	98.79	**125**	0.01	99.96
24	1.08	74.19	**58**	0.28	93.53	**92**	0.07	98.86	**126**	0.01	99.97
25	1.01	75.20	**59**	0.28	93.81	**93**	0.07	98.93	**127**	0.01	99.97
26	0.96	76.16	**60**	0.27	94.08	**94**	0.07	98.99	**128**	0.01	99.98
27	0.91	77.07	**61**	0.26	94.34	**95**	0.06	99.06	**129**	0.01	99.99
28	0.90	77.97	**62**	0.24	94.58	**96**	0.06	99.12	**130**	0.01	100.00
29	0.84	78.81	**63**	0.23	94.81	**97**	0.06	99.17			
30	0.80	79.61	**64**	0.22	95.03	**98**	0.05	99.22			
31	0.78	80.39	**65**	0.21	95.24	**99**	0.05	99.27			
32	0.73	81.12	**66**	0.21	95.45	**100**	0.05	99.32			
33	0.72	81.84	**67**	0.20	95.65	**101**	0.05	99.37			
34	0.70	82.53	**68**	0.19	95.84	**102**	0.04	99.41			

Table 6.8 Melanesian and Australia: Cross validation study to assess the separation by proportion of sample variance

Sample	70% (PCs 1-21)	80% (PCs 1-31)	90% (PCs 1-48)	95% (PCs 1-64)	100% (PCs 1-130)
ANG	52.63%	57.89%	73.68%	68.42%	57.89%
KNG	55.56%	50.00%	50.00%	38.89%	16.67%
SNG	38.10%	38.10%	52.38%	61.90%	42.86%
NB	68.57%	82.86%	77.14%	71.43%	31.43%
SI	38.10%	43.86%	42.86%	57.14%	38.10%
NC	40.00%	46.67%	53.33%	53.33%	26.67%
NSW	41.67%	66.67%	58.33%	58.33%	33.33%
Saus	62.52%	56.25%	50.00%	31.25%	31.25%
Tas	58.33%	66.67%	41.67%	41.67%	25.00%
Mean	**50.61%**	**56.44%**	**55.49%**	**53.60%**	**33.69%**

Table 6.9 Mahalanobis' D distance matrix: Melanesia and Australia; * significant at $p \leq 0.05$
ANG, Awaiawama (New Guinea); KNG, Kwaiawama (New Guinea); SNG, Sinaugolo (New Guinea); NB, New Britain; SI, Solomon Islands; NC, New Caledonia; NSW, New South Wales; SAus, South Australia; Tas, Tasmania.

	ANG	KNG	SNG	NB	SI	NC	NSW	SAus	Tas
ANG	0.00								
KNG	12.11*	0.00							
SNG	9.13*	10.46*	0.00						
NB	22.83*	16.94*	19.30*	0.00					
SI	16.64*	11.97*	8.08*	15.93*	0.00				
NC	15.97*	13.62*	19.11*	9.61*	21.10*	0.00			
NSW	18.92*	17.78*	13.20*	21.55*	11.94*	23.00*	0.00		
SAus	26.14*	21.04*	17.62*	20.51*	16.11*	27.01*	9.90*	0.00	
Tas	18.42*	20.84*	13.68*	25.43*	13.70*	30.93*	14.35*	13.36*	0.00

The Mahalanobis' D distances between the samples are given in table 6.9. The smallest distance between any two groups remains between the Solomon Islands and the Sinaugolo sample from New Guinea (D = 8.05). The largest distance is found

between the New Caledonia and Tasmanian samples (D = 30.93). All distances are significant at $p \leq 0.05$.

The results of the cross validation analysis are given in table 6.10. The addition of the Australian samples results in a lower mean number of correctly classified OTUs than when only the Melanesian samples are included, though given that the number of samples is increased this is not a surprising result. Only 56.4% of individuals are correctly placed in their original groups. Again, the least number of correctly placed individuals are from the Sinaugolo, New Guinea, sample, with only 38.1%. The misclassified individuals from this sample are placed in the Awaiama, New Guinea, and the Solomon Islands samples. Similarly, the Solomon Islands sample has a large number of misclassified individuals placed in the Sinaugolo sample. Of the Melanesian samples, only the Solomon Islands have more than one individual misclassified in an Australian sample. The highest correct classification is found in the New Britain sample, with 82.9% correctly placed individuals. There is no statistical correlation between the number of individuals in each sample and the percentage of correct classification in this analysis.

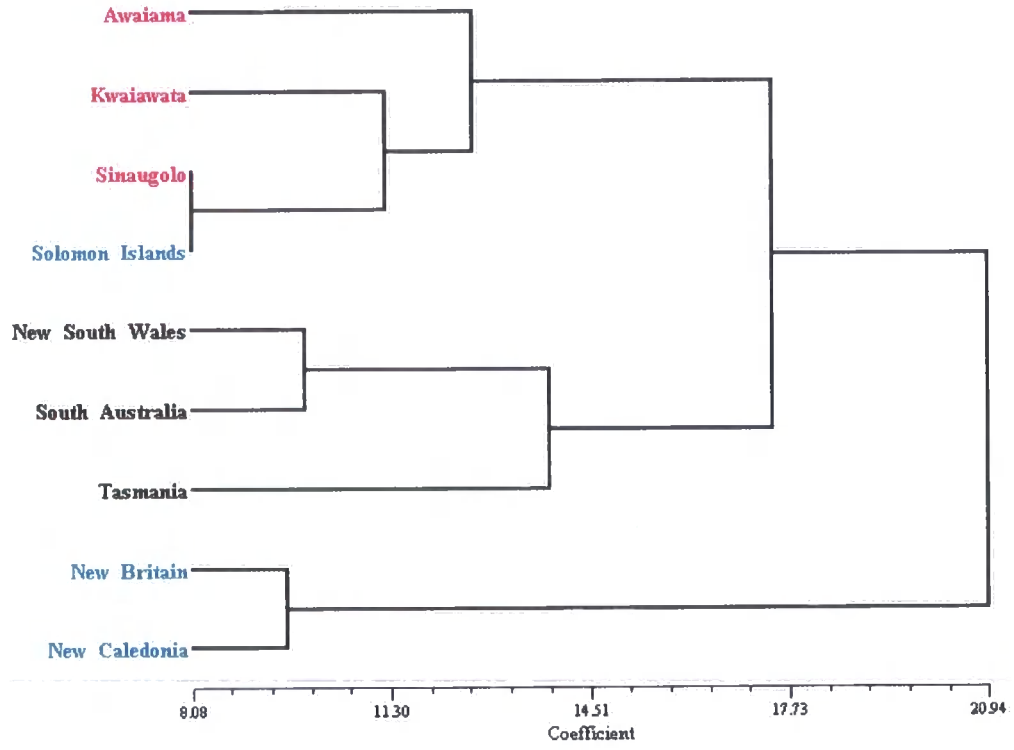
Table 6.10 Cross validation analysis: Melanesia and Australia.
ANG, Awaiawama (New Guinea); KNG, Kwaiawama (New Guinea); SNG, Sinaugolo (New Guinea); NB, New Britain; SI, Solomon Islands; NC, New Caledonia; NSW, New South Wales; SAus, South Australia; Tas, Tasmania.

	ANG	KNG	SNG	NB	SI	NC	NSW	SAus	Tas	Total
ANG	**57.89**	15.79	10.53	0.00	5.26	5.26	0.00	0.00	5.26	100.00
KNG	11.11	**50.00**	11.11	0.00	16.67	5.56	0.00	0.00	5.56	100.00
SNG	19.05	9.52	**38.10**	0.00	23.81	0.00	4.76	0.00	4.76	100.00
NB	0.00	0.00	2.86	**82.86**	2.86	11.43	0.00	0.00	0.00	100.00
SI	0.00	9.52	19.05	9.52	**42.86**	0.00	14.29	0.00	4.76	100.00
NC	6.67	13.33	6.67	26.67	0.00	**46.67**	0.00	0.00	0.00	100.00
NSW	8.33	0.00	0.00	0.00	8.33	4.17	**66.67**	8.33	4.17	100.00
SAus	0.00	0.00	6.25	6.25	0.00	0.00	18.75	**56.25**	12.50	100.00
Tas	0.00	0.00	16.67	0.00	8.33	0.00	0.00	8.33	**66.67**	100.00

The phenogram produced from the Mahalanobis' D distances is presented in figure 6.9. The addition of the Australian samples emphasises the distinctiveness of the

New Britain and New Caledonian samples, with these being placed on a separate branch from the remaining groups. The Australian samples form a separate cluster following the second bifurcation. The clustering of the New Guinea samples with the Solomon Islands sample, as illustrated in figure 6.4, remains constant in this phenogram. Within the Australian cluster, the New South Wales and South Australian samples are more similar to one another, with the Tasmanian sample as an outlier from the two mainland Australian samples.

Figure 6.9 Phenogram showing shape relationships between the Melanesian and Australian samples.



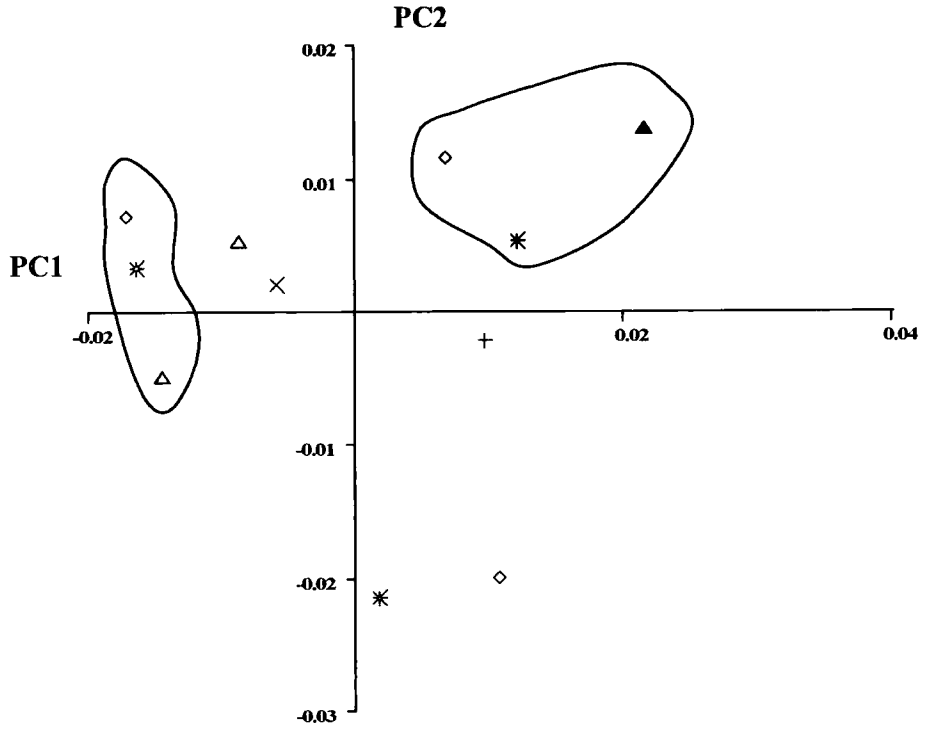
6.4.2a Craniofacial diversity in Melanesia and Australia: Means

The craniofacial diversity found within the Melanesian and Australian samples is further explored using the sample means. As with the sample mean analysis in section 6.4.1a, the Louisiade Archipelago and Loyalty Islands samples are added to the analyses. The new data set is submitted to Procrustes fitting and the results of the principal components analysis (PC1 versus PC2) are shown in figure 6.10. Only PC1 versus PC2 produced recognisable separation of the population samples. PC1 explains 24.9% of the total sample variance and PC2 a further 18.8%. Table 6.11 lists the percentage variance and cumulative percentage given by each PC.

Table 6.11 Melanesia and Australia sample means: The proportion and accumulated variance of PCs 1 – 10, which account for 100% of total sample variance

Principal Component	Variance %	Cumulative Variance %
1	24.9	24.9
2	18.8	43.7
3	12.9	56.6
4	10.5	67.1
5	8.5	75.6
6	7.8	83.4
7	5.3	88.7
8	4.4	93.1
9	3.8	96.9
10	3.1	100.0

Figure 6.10. Melanesia and Australia: PC 1 v PC 2



◇ Awaiama
△Kwaiawata
✳ Sinaugolo
◇New Britain
△ Solomon Islands
✳ New Caledonia
× Louisiade Archipelago
\+ Loyalty Islands
◇ New South Wales
▲ South Australia
✳ Tasmania

Figure 6.10 identifies a separation across the axis of PC1 between the New Guinean samples (circled), towards the negative extreme, and the Australian samples (circled) which have positive scores on this axis (figure 6.10). The Melanesian samples are situated between the two extremes of the axis. The mean shape configurations at the negative and positive extremes of PC1 are illustrated in figure 6.11. Warping from the negative to the positive extreme of PC1 there is a relative decrease in facial height (figure 6.11 i), with a relatively more posteriorly positioned mid face (figure 6.11 ii). Basicranial length also increases relatively (figure 6.11 iii) and the face becomes relatively more compact with an anterior and superior displacement of the alveolar surface (figure 6.11 iv).

Along PC2 there is a distinct separation between the grouping of the New Britain and New Caledonia samples and all other samples (figure 6.12). The morphological variation along PC2 is clearly being driven by this separation, with the samples at the negative extreme being characterised by a relative posterior slope of the face (figure 6.12 i) and a pronounced prognathism of the maxillary region (figure 6.12 ii). Warping from the negative extreme of PC2 to the positive, there is a more relative anterior placement of glabella (figure 6.12 iii) associated with a relative flattening of the face (figure 6.12 iv). The New Britain and New Caledonia samples are thus defined morphologically by their relatively pronounced lower maxillary prognathism and a more relatively posteriorly sloping face than the remaining Melanesian and Australian samples.

Figure 6.11 PC1 TPS: Differences in shape along the first PC. The upper figure represents the mean landmark configuration warped along PC1 from the negative to the positive extreme

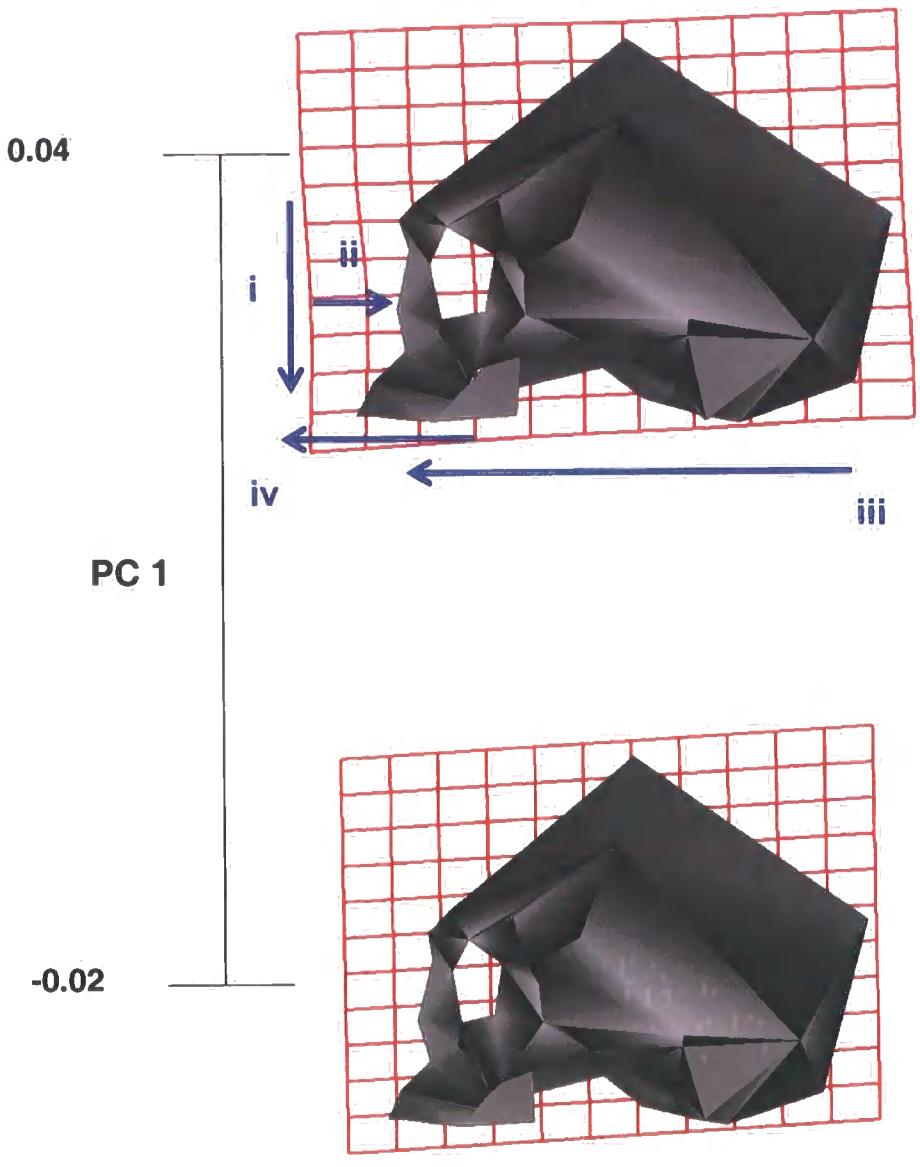
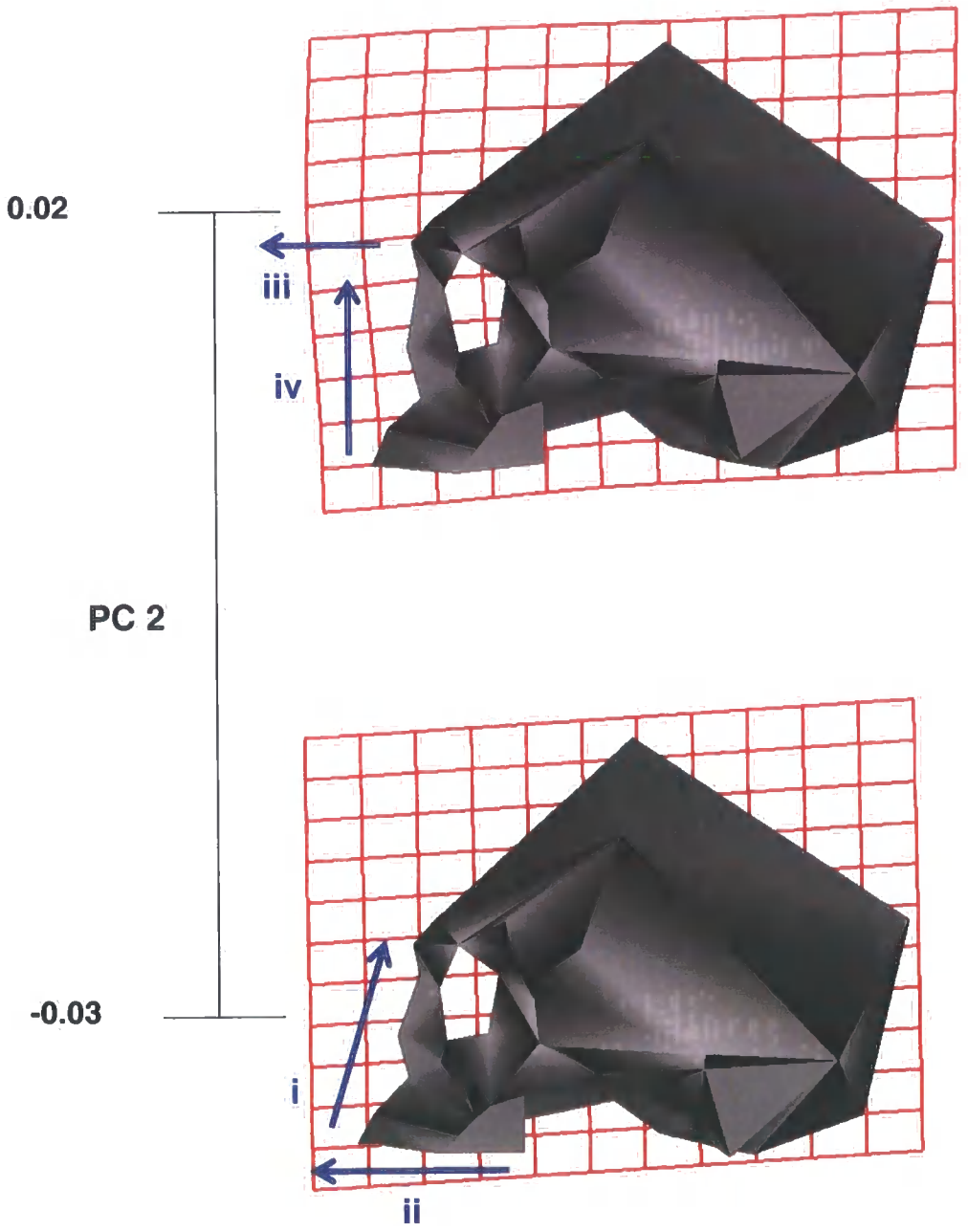


Figure 6.12 PC2 TPS: Differences in shape along the second PC. The upper figure represents the mean landmark configuration warped along PC2 from the negative to the positive extreme



6.5 Discussion

6.5.1 Craniofacial diversity in Melanesia

As with South and Southeast Asia, Melanesia has a long and complex history of migration into the region, starting with the Late Pleistocene dispersal out of Africa and continuing in the Holocene with the Lapita cultural expansion (Kirch, 2000). This has led to the region being described as having no cultural or historical unity and displaying great genetic and linguistic diversity (Kirch, 2000). The first analyses undertaken in this chapter were to assess the patterns of morphological variation within these islands. In agreement with the genetic and linguistic data, craniofacial diversity between the different samples is demonstrated by the statistically significant Mahalanobis' distances between them (table 6.4). This diversity is further reflected in the cross validation results that placed 60.4% of all Melanesian individuals into their original population groupings (table 6.5). All but two of the sample populations achieved over 60% correct classification of individuals in the discriminant analysis, demonstrating further that on the whole the samples are distinct from one another. The diversity thus described by Kirch (2000) is seen to be reflected in the craniofacial skeleton of the Melanesian sample in this study. The first null hypothesis, $\mathbf{H_1}$, that the populations of the different islands of Melanesia are not morphologically distinct from one another, is therefore refuted.

Melanesia plays an interesting role in the proposed southern route hypothesis as it is one of the terminal points of the Late Pleistocene migration, with a clear distinction between the islands settled at this time and those not settled until during the Holocene (Kirch, 2000). Having demonstrated that morphological differences exist between the samples from the various islands of New Guinea and Melanesia, the chapter aimed to further explore the craniofacial diversity found in relation to the proposed settlement pattern of the region. The most simple interpretation of the settlement history of Melanesia is that the first colonists arrived around 45,000 BP and then no further incursions occurred until the Lapita expansion during the Holocene (O'Connell and Allen, 2004). Green (1991) described Melanesia as having two discrete regions, Near and Remote Oceania, which represent two major epochs in the population history of the region. Near Oceania consists of New Guinea and the islands as far south and east as the Solomon Islands (figure 6.2) and the initial Late Pleistocene dispersal only reached as far as these islands. Near

Oceania therefore has had a much longer history of occupation than Remote Oceania and the populations have had a greater length of time in which to diversify. The second null hypothesis addressed the question of whether the geographical and historical split between Near and Remote Oceanic populations is also identifiable in their craniofacial morphology. The results show that no such split is readily identifiable in the craniofacial skeleton of the samples from Near and Remote Oceania. The Mahalanobis' distances, for example, between the Near and Remote Oceanic samples are not the largest distances found within the matrix, as would have been expected if this split was evident today. The patterns of craniofacial variation are more complex than simply following the migratory history of the region. The craniofacial diversity appears, rather, to be driven by the close morphological affinity between New Britain and New Caledonia samples. This affinity is evident from both the phenogram (figure 6.4) and the PCA of the sample means, although geographically the locations of the samples are from alternate ends of Island Melanesia. The principal components analysis of the sample means additionally illuminates the complex relationships between Near and Remote Oceania. No clear and simple split in morphology is found between the two regions. Null hypothesis, $\mathbf{H_2}$, stating that the samples from the Islands of Near Oceania are not morphologically distinct from those of Remote Oceania, is therefore supported. No clear evidence of the Late Pleistocene migration is found in the populations of Melanesia. The historical split between Near and Remote Oceania is not reflected in the craniofacial morphology of the extant populations. This result may not be so surprising given the demographic history of Melanesia from the Holocene onwards.

Near Oceanic populations are renowned for their genetic diversity and the common explanation given is that this variability among islands is the result of ancient human settlement and subsequent small population isolation (Robledo *et al.*, 2003). The genetic diversity is echoed in craniofacial morphology, but for the whole of Melanesia rather than only Near Oceania. The craniofacial similarities between the New Britain and the New Caledonia samples appears to be the driving force in creating the complex patterns found in the present study. Current archaeological evidence does not provide a simple answer to why these two islands have such a similar morphology (Spriggs, pers. comm.). The morphology displayed by New Britain and New Caledonia is characterised by the extreme prognathism of the

maxilla (figure 6.6) and this may suggest a functional explanation as a cause of the similarities, with the extended maxilla being a response to a particular biomechanical strain. Experimental research has demonstrated that the maxilla and palate structures are plastic in relation to diet consistency (Giesen *et al.*, 2003). A shared dietary custom may therefore explain the similarities between these two samples. Again, however, there are no present data that can help to determine similar environmental conditions or a shared resource strategy that would create such a biological stress. There is little evidence to suggest a similarity in ecology between the two islands in question, to the exclusion of other Melanesian island groups, which may rule out evolutionary adaptation as the causal factor for the shared morphology. A more simple explanation would be that similarities exist due to population dispersals, despite the distance between the islands. During the mid to late Holocene, New Britain is known to have experienced the effects of up to thirteen eruptions of the Witori volcano and four from the Dakataua volcano (Torrence *et al.*, 2000). These eruptions led at times to the abandonment of settlements on New Britain, giving rise to the opportunity for colonisation by external populations. This is, of course, speculation as no known specific links exist between New Britain and New Caledonia beyond the later proposed dispersals of people during the Lapita cultural expansion. A further speculative reason for the similar craniofacial morphology between the New Britain and New Caledonia samples could be the retention of an ancestral shape in both these regions. New Caledonia is one of the most westerly islands in Remote Oceania and may have been occupied early during the Lapita expansion, possibly from New Britain. If no further migration to New Caledonia occurred founder effect could have assisted the retention of a morphology shared by the ancestral population.

Although current data does not allow for a clear explanation of this shared craniofacial shape across a wide geographic distance, the concurrence of this morphology between the two islands demonstrates the complex biological patterns that are found throughout Melanesia. The patterns of craniofacial morphology found in extant populations are the products of long historical occupation and extended migrations into the area. It would therefore be beneficial to explore craniofacial morphology over time as well as space. Little skeletal material has been available for study that dates to the period of the Lapita expansion (Bedford *et al.*, 2006).

Excavations at the Teouma Lapita cemetery on Vanuatu, however, should provide relevant material for such study (Bedford *et al.* 2006). Twenty five skeletons have been excavated so far from this site and analysis of such material would greatly add to the knowledge of the evolution of Melanesian craniofacial morphology.

6.5.2 Craniofacial diversity in Melanesia and Australia

During the time of the initial settlement of the continent, New Guinea and Australia were connected to each other as part of Sahul. It has been claimed, therefore, that the indigenous peoples of these regions result from the same ancient migration and share a distant common ancestor (Bellwood, 1978). The set of analyses in the second section of this chapter, therefore, explored the nature of the relationships in craniofacial shape between Melanesia and Australia. Any morphological similarities between the samples may reflect a common ancestry of these populations. Distinct differences in craniofacial morphology between Melanesian and Australian samples are shown by the statistically significant Mahalanobis' distances between the samples (table 6.9). The null hypothesis, $\mathbf{H_3}$, stated that the populations of Melanesia are not morphologically distinct in craniofacial shape from Australian Aboriginal populations, and is therefore refuted. The refutation of the hypothesis, however, does not definitively rule out a shared ancestry for the two populations. Some similarity of shape is evident between the Melanesian and Australian samples. Over 50% of all individuals were correctly classified in the discriminant analysis (table 6.10) for example. This percentage is lower than when only Melanesian samples are included in the analysis, demonstrating that there is some overlap in craniofacial shape between the Melanesian and Australian samples. Additionally no clear separation of the Melanesian and Australian samples is evident on the phenogram (figure 6.9) or on the sample means PCA graph (figure 6.10). Both of these figures do, however, illustrate once more the distinctive shape of the New Britain and New Caledonian samples, as discussed above.

It is evident that no simplistic morphological relationship exists between the Australian and Melanesian samples in this study. Although statistically different, some similarity of shape can be identified, for example as evident by only subtle differences being observed on PC2 of the sample means PCA (figure 6.10). Similarity of shape could suggest that the samples have diverged from a common

ancestral morphology in the past. Support for a shared common ancestry comes from the mitochondrial DNA haplotypes P and Q, which are recognised as being specific to the Southwest Pacific region (Merriwether *et al.*, 2005). The haplogroup clusters, however, propose a substantial isolation of Australia from Melanesia since around the time of the first settlement of the region. All but one of the branches of the P haplotype, occur either in Australia only or only in New Guinea. Q is absent in Australia but very common in New Guinea and Island Melanesia (Merriwether *et al.*, 2005). This period of isolation would be enough for morphological diversification as found in these analyses to occur due to the processes of drift and local adaptation. The results of Chapter 4 illustrate the plastic nature of craniofacial morphology that can be affected by specific environmental conditions.

In the wider context of Oceania, the Australian samples in this study cluster together as a homologous group. Within the samples, however, there are statistically significant differences, showing that there are regional morphologies within Australia itself. These differences have been attributed in the past to multiple migrations into the island, and in the case of Tasmania, due to the long period of isolation following the flooding of the Bass Strait. As with the differences between the Melanesians and the Australians, the diversity found within Australia does not necessarily indicate differing waves of migration bringing with them new morphological types. The fact that the Australian samples are more like one another than any external sample suggests it is more likely that they have diversified from a common ancestral morphology by the processes of drift and adaptation. Lahr (1996) states that a long period of comparative isolation could have led to the overall similarity found between recent and fossil Australian cranial remains. This finding would support the unitary model of Pardoe (2006) in which evolutionary processes are responsible for structuring human variation throughout the continent, from the earliest known remains to modern peoples. In this model Pardoe (2006) stresses that there is no need to invoke multiple founder populations and migration scenarios to account for the observed population variation. Rather diversification is developed by the operation of gene flow, adaptation and genetic drift in particular environmental contexts. Reproductive isolation, for example, as a result of specific marital patterns can be a causal factor of the observed biological diversity (Pardoe, 2006).

'Australo-Melanesians'

A final point resulting from the analyses in this section is related to the descriptions of the Australians and Melanesian populations. A number of researchers refer to these populations as a single typological group, the 'Australo-Melanesians' (eg. Howells, 1989; Hanihara, 1993, Pietrusewsky, 2006). The term is commonly used to refer to either the recent indigenous people of Australia, New Guinea or Island Melanesia or prehistoric populations from Southeast Asia. The results of this study demonstrate that the heterogeneity of the craniofacial skeleton in the Melanesian and Australian samples makes it inadvisable to pool them for morphometric analysis. Such pooling is common in current craniometric analsyses (e.g Howells, 1989; Bellwood, 1997; Pietrusewsky, 2006). The results indicate that there are more complex relationships in craniofacial shape than is suggested by a simple 'Austro-Melanesian' grouping. The distinct distributions of the P and Q mtDNA haplotypes identified further contradict the early notions of a loosely unified Melanesian, Australoid or Austro-Melanesian population (Merriwether et at., 2005). The statistically significant differences between the Melanesian and Australian samples utilised here, combined with the known diversity in genetics within Oceania, suggest that the 'Austro-Melanesian' concept is no longer valid. The morphological complexity of the region combined with the intricate demographic and evolutionary processes that have determined this morphology call for the individuality of the regional groupings to be recognised.

6.5.3 Summary of craniofacial shape variation within Melanesia and Australia

The combined results of this chapter conclude that the geographic region including Australia and Oceania has an extremely complex pattern of craniofacial morphological diversity. The extended history of the region, going back approximately 40,000 years, has created a very varied picture, resulting from dispersals from diverse and as yet inconclusive origins, from long term isolation of the region, from genetic drift and from founder effect. The initial migration into the region revealed by archaeological evidence is not explicitly reflected in the craniofacial morphology of the present day inhabitants. Subsequent migrations and dispersals have overlain the original settlement pattern and evolutionary effects have added to the diversity found today. The craniofacial morphology of the region, however, is not without discernable patterns. There is a strong morphological

association between the New Britain and New Caledonian samples that is not easily explained by the proposed migratory history of the region. Genetic research into the samples from these islands would assist the exploration of similarities found in craniofacial shape between these areas and assess whether the impact of natural disasters could be a possible cause or whether functional explanations are more parsimonious. Similarly, the Australian samples can be seen as a phenotypic unit, with enough difference from the Melanesian samples to refute the coinage of the term 'Australo-Melanesian'. Overall, the known migratory history of Australia and Oceania, starting in the Late Pleistocene and developing throughout the Holocene, is not readily discernable from the craniofacial morphology of the present day inhabitants. Patterns exist but further genetic and archaeological evidence is required to assess the possible driving forces behind the morphological diversity of the Melanesians and their immediate neighbours.

- The historical split between Near and Remote Oceania is not reflected in the craniofacial morphology of the samples from these regions

- Samples from New Britain and New Caledonia share a similar craniofacial morphology characterised by maxillary prognathism

- A shared ancestral population between Melanesians and Australians cannot be accepted or refuted by the evidence of these samples

- The Australian samples form a distinct morphological cluster

- The complex pattern of diversity found within the samples rejects the general notion of an 'Australo-Melanesian' complex.

Chapter 7

Craniofacial Diversity in Polynesia

7.1 Introduction

The preceding chapters have examined craniofacial diversity as evidence of the Late Pleistocene dispersal out of Africa along the proposed southern route. Patterns of variation and possible causes of the observed diversity have been discussed. As covered in Chapter 6, the Late Pleistocene dispersal had an eastern demarcation at the Solomon Islands, and the islands of Remote Oceania, including Polynesia, were not occupied until approximately 40,000 years later. The present chapter extends the discussion of craniofacial diversity and dispersal geographically eastwards, and temporally forwards into the Holocene, to one of the last areas to be settled by *Homo sapiens*. The rapid settlement of Polynesia provides an interesting comparison to the more slow and mosaic settlement of the proposed southern route.

7.1.1 Craniofacial diversity in Polynesia

Polynesia consists of the area of the Pacific bounded by Fiji to the west, Hawaii to the north, Easter Island to the east and New Zealand to the south (figure 7.1). Expansion into Remote Oceania began around 3,500 BP, with the expansion of the Lapita cultural complex and the Austronesian linguistic family (Kirch, 2000). Archaeological evidence suggests that western Polynesian islands, including Fiji and Samoa, were settled by around 3,200 – 2,100 years ago (Kayser *et al.*, 2006). By 1,000 BP, all the major island groups of eastern Melanesia, Micronesia and Polynesia had been colonised (Green, 1991). Due to constraints of sample size, the Polynesian population samples represented in this chapter come from New Zealand, Easter Island, Hawaii and the Chatham Islands.

It is thought that New Zealand was colonised by about 1200 AD, based on radiocarbon dating of seeds gnawed by the Polynesian rat (*Rattus exulans*) that arrived alongside the human settlers (Wilmshurst and Higham, 2004). New Zealand is temperate, the only part of Polynesia lying outside of the tropical-sub-tropical zone in which ancestral

Polynesian culture developed. The Chatham Islands were settled shortly after this time by a group from New Zealand (Sutton, 1980). Evidence from the mtDNA of Polynesian rats on the Chatham Islands suggests that the colonisation of these remote islands occurred only once and that they were thereafter isolated until European contact during the eighteenth century (Matisoo-Smith *et al.*, 1998). The indigenous Chatham Islanders, called Moriori, were largely exterminated by the Maori from New Zealand in a raid in 1835. Easter Island was also settled around 1200 AD and is the world's most isolated inhabited island (Hunt and Lipo, 2006). Easter Island is situated in Eastern Polynesia, 2,300 miles west of South America and 4,300 miles south of Hawaii. The exact date of the colonisation is uncertain, but some archaeologists suggest around 750-800 AD or possibly slightly earlier (Kirch, 2000). The Hawaiian islands are second only to New Zealand in size and enjoy a subtropical climate, though the individual islands vary greatly in their environmental characteristics. After about 1,300 AD long distance voyaging from Hawaii ceased and the islands of Hawaii became completely isolated from the rest of Polynesia (Kirch, 2000). A general theme of the Polynesian islands is that following settlement, most were subsequently isolated, to differing extents, from outside human contact.

Previous research suggests that morphologically, the present day inhabitants of Polynesia are a relatively homogenous group when compared with other Oceanic populations (Howells, 1970). Houghton (1996) stresses many morphological features that denote a common Polynesian phenotype, such as large body size and a high incidence of the 'rocker jaw'. Skeletal studies using both metric and non metric traits produce groupings in which Polynesian samples consistently link more closely with each other than with external populations (Howells, 1970; Pietrusewsky, 1994). A likely explanation for this high degree of biological homogeneity, seen at both a molecular and morphological level, is that the parental population from which all Polynesian groups derive went through a series of 'bottlenecks' during Oceanic settlement (Lum *et al.*, 2002). Following this bottleneck, extensive gene flow primarily focused among neighbouring populations is indicated by a robust correlation between genetic and geographic distances (Lum *et al.*, 2002).

The human settlement of the Pacific and the origins of the Polynesians in particular, have been debated for many years. Polynesian origins can be traced to the people who arrived in the Fiji, Tonga and Samoa region around 3,000 BP and are clearly associated with the Lapita cultural complex (Matisoo-Smith and Robins, 2004). Whilst this initial movement into Remote Oceania is generally accepted, the ultimate origins of the Polynesians and the Lapita culture continue to be contentious. Linguistic evidence suggests an Asian origin of the Polynesians, as their languages are closely related to one another and belong to the Austronesian language family that ultimately had its source in Taiwan (Blust, 1996). Archaeological evidence, however, points to an origin of Polynesian ancestors within Melanesia, by people associated with the Lapita cultural complex. The Lapita cultural complex is generally thought to have originated between 3,500 – 3,000 years ago in the Bismarck Archipelago (Kirch, 2000). Some archaeologists argue, however, that the Lapita cultural complex actually originated in China around 6,000 years ago and that its spread is associated with that of farming (Bellwood, 1978). This is also linked with the spread of the Austronesian languages and is used to support the 'Express Train' model for the origins of the Polynesians (Gray and Jordan, 2000). The 'Express Train' model, also known as the 'Out of Taiwan' model, proposes a rapid migration of Austronesian speaking peoples into Island Southeast Asia from Taiwan beginning about 5,500 years ago (Bellwood, 1991, 2000). Under this model the Lapita sites in Near Oceania are viewed as evidence of an intrusive 'Austronesian' settlement. Early descriptions of this model suggested little interaction between the settlers and the existing inhabitants of Near Oceania (Diamond, 1988), but more recent formulations allow for more integration (Green, 2003).

In contrast to the evidence that suggest an Asian origin for Polynesian languages and a probable Melanesian origin of the Lapita material culture found in Polynesia, the genetic origin of the Polynesians is less clear (Kayser *et al.*, 2006). Although an Asian origin has been favoured by mtDNA studies, giving further support to the 'Express Train' scenario (Trejaut *et al.*, 2005), studies of Y chromosome data have revealed a predominantly Melanesian origin of Polynesian paternal lineages (Kayser *et al.*, 2000;

Capelli *et al*, 2001). These findings support a 'Slow Boat' model in which Polynesian ancestors originated in Taiwan or East Asia but mixed extensively with indigenous Melanesians before colonising the Pacific (Kayser *et al.*, 2000). Under this model a dual genetic heritage of Polynesians is proposed, with contributions from both Melanesian and Asian genetic components (Kayser *et al.*, 2006). When mtDNA and Y chromosome data were explicitly compared, differential proportions of the genetic components were found from Melanesian and Asian haplogroups (Kayser *et al.*, 2006). The comparative data suggested a pronounced admixture bias in Polynesians toward more Melanesian men than women, perhaps due to matrilocal residence in ancestral Polynesian society (Kayser *et al.*, 2006; Hage and Marck, 2003).

A contrary view to the ultimate Taiwanese origin of Polynesians holds that the colonisation of Remote Oceania has its origins in the Bismarck Archipelago, as suggested by the archaeological evidence (Terrell *et al.*, 2001). According to this 'Entangled Bank' model, the Lapita culture arose in the Bismarck Archipelago as a product of long term human interaction, starting from the first Pleistocene occupation of Melanesia. No major intrusive expansion of Austronesian speaking populations from Island Southest Asia need be considered to account for the appearance of the Lapita cultural complex (Terrell *et al.*, 2001). The new culture, and associated burst of colonisation that resulted in the settlement of Polynesia, is assumed to have arisen from an ongoing cultural and biological mix leading to new ideas and technical innovations. Any long term bottlenecks detected in descendent populations are suggested as being the result of in situ changes within the populations rather than migrational events (Cann and Lum, 2004).

A final model, the 'Voyaging Corridor' or 'Slow Boat to Polynesia' model places Polynesian ancestors among the populations coming from the seafarers of Island Southeast Asia, somewhere between Wallace's line and New Guinea (Oppenheimer and Richards, 2001). This model supposes that the drowning of the Sunda shelf around 15,000 – 7,000 years ago forced Austronesian speaking, coastal, Southeast Asian agriculturalists to move into northern Melanesia (Oppenheimer, 1999). An intermediate

passage in coastal Melanesia is implied by this model, with a certain degree of admixture between local populations and Polynesian ancestors. Evidence from *Alu* insertion polymorphisms from Easter Island provides support for the 'Voyaging Corridor' model, suggesting the pre-Polynesians are mainly derived from Southeast Asian and Wallacean populations rather than Taiwan (González-Pérez *et al.*, 2006).

Hypotheses

Much of the debate about the origins of the Polynesians is thus concerned with the relative contributions to the region from Island Southeast Asia and Near Oceania. Although various models exist to explain the origins of the Polynesians, there is little consensus between them. This chapter will thus assess the craniofacial diversity of the Polynesians in relation to these regions in order to ascertain whether any continuity can be identified with these groups. The following null hypothesis is constructed:

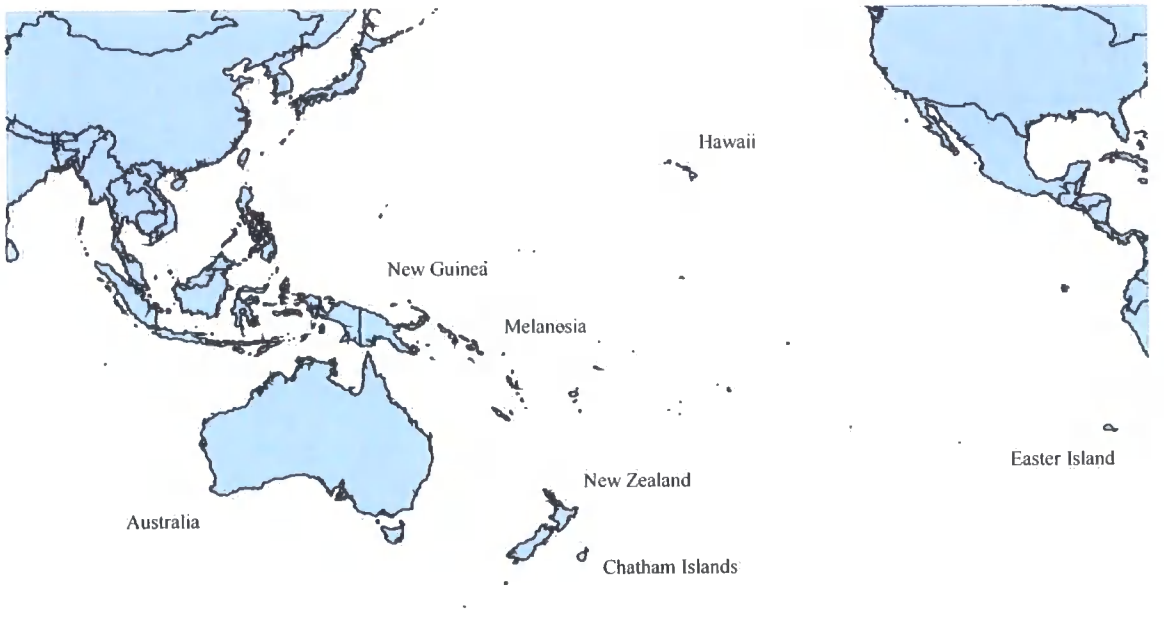
H_1 "The populations of Polynesia are not morphologically distinct in craniofacial shape from populations from Southeast Asia and Melanesia"

Statistically significant differences between the samples will lead to the hypothesis being refuted.

7.2 Materials

The materials in this study represent sub-sets of extant populations that are found in Melanesia, Southeast Asia and Polynesia. The samples consist of mixed sex specimens. Table 7.1 summarises the sample sizes for each population. Samples marked ** are used in the analyses of sample means only, due to their small sample size. Further details of the provenance of these specimens, assessment of maturation and determination of inclusion can be found in the materials section of Chapter 2.

Figure 7.1 Map of Island Southeast Asia, Melanesia and Polynesia



7.3 Methods used in this chapter

Biological Distances

The degree of discrimination in shape between the groups is measured using Mahalanobis' D for the complete samples. Mahalanobis' D, or generalised distance, is a function of the group means and the pooled variances and covariances among populations. Mahalanobis' D is used to test whether group centroids are significantly different and the discriminatory power of that distance. To measure the differences between the means of population samples, Procrustes distances were utilised. The distance is approximately the square root of the sum of squared differences between the positions of the landmarks after GPA.

Discriminant Analysis

Discriminant analysis with crossvalidation is used to classify individuals into predefined groups, based upon Mahalanobis' D^2 distances. Each individual is assigned a probability of belonging to a given group based on the distance of its discriminant function from that of each group mean. Crossvalidation is employed as it provides a better assessment of classification accuracy than standard discriminant analysis. During crossvalidation, classification is carried out for each individual in turn and the discriminant function used in each case is constructed with that individual removed. The crossvalidation analyses are carried out using SAS (The SAS Institute Inc., 1996).

Correlations

Regression analysis is undertaken using Pearson's correlation coefficient (r) and associated p-value. Values are calculated using the statistical software package SPSS (SPSS for Windows, Rel. 14.0.2. 2006. Chicago: SPSS Inc.).

Distance Phenograms

Utilising the Mahalanobis' distances and Procrustes distances, UPGMA phenograms were constructed in order to summarise the morphological relationships between the groups. The phenograms were created using the program NTSYS (Exeter Software).

Geographic measures of distance

Minimum geographic distances between the samples are calculated from the latitude and longitudinal coordinates of the samples, as described in Chapter 3.

Table 7.1. Southeast Asia, Melanesia and Polynesia: Composition of data sets

Region	Country	Sample	Sample Size	Specimen Location*
Southeast Asia				
	Borneo	Borneo	35	NHM, O, DC
	Java	Java	17	NHM, O
	Sulawesi	Sulawesi**	5	NHM
	Moluccas	Moluccas**	6	NHM
	Sumatra	Sumatra**	6	NHM, DC
	Timor	Timor**	7	NHM
Melanesia				
	Papua New Guinea	Awaiama	19	DC
	Papua New Guinea	Kwaiawata	18	DC
	Papua New Guinea	Sinaugolo	21	NHM, DC
	New Britain	New Britain	35	NHM, DC
	Solomon Islands	Solomon Islands	21	NHM, O, DC
	Louisiade Archipelago	Louisiade Archipelago**	10	NHM, O
	New Caledonia	New Caledonia	15	NHM, DC
	Loyalty Islands	Loyalty Islands**	7	NHM
Polynesia				
	Easter Island	Easter Island	29	NHM
	Chatham Islands	Chatham Islands	35	NHM, DC
	New Zealand	New Zealand	21	NHM
	Hawaii	Hawaii**	8	NHM, O
Total			**307**	

* NHM, Natural History Museum, London; O, The University Museum of Natural History, University of Oxford: DC, The Duckworth Laboratory, University of Cambridge.

** Used only in the analyses of sample means.

7.4 Results

7.4.1 Craniofacial diversity in Melanesia and Polynesia

Principal components analysis is conducted on the Procrustes fitted data on samples from Island Southeast Asia, Melanesia and Polynesia (see table 7.1). The principal component scores for the total sample variance are given in table 7.2. PC1 explains 12.5% of the total sample variance and PC2 9.1%. No clear separation of the samples is provided by any single PC (figure 7.2). Comparisons of discriminant analyses are performed to assess the effects of noise factors in the analyses (table 7.3). Using approximately 95% of the total variance produces the optimal discrimination and thus the remaining analyses in this section are carried out using PCs 1-68.

Figure 7.2. Melanesia and Polynesia: PC 1 v PC 2

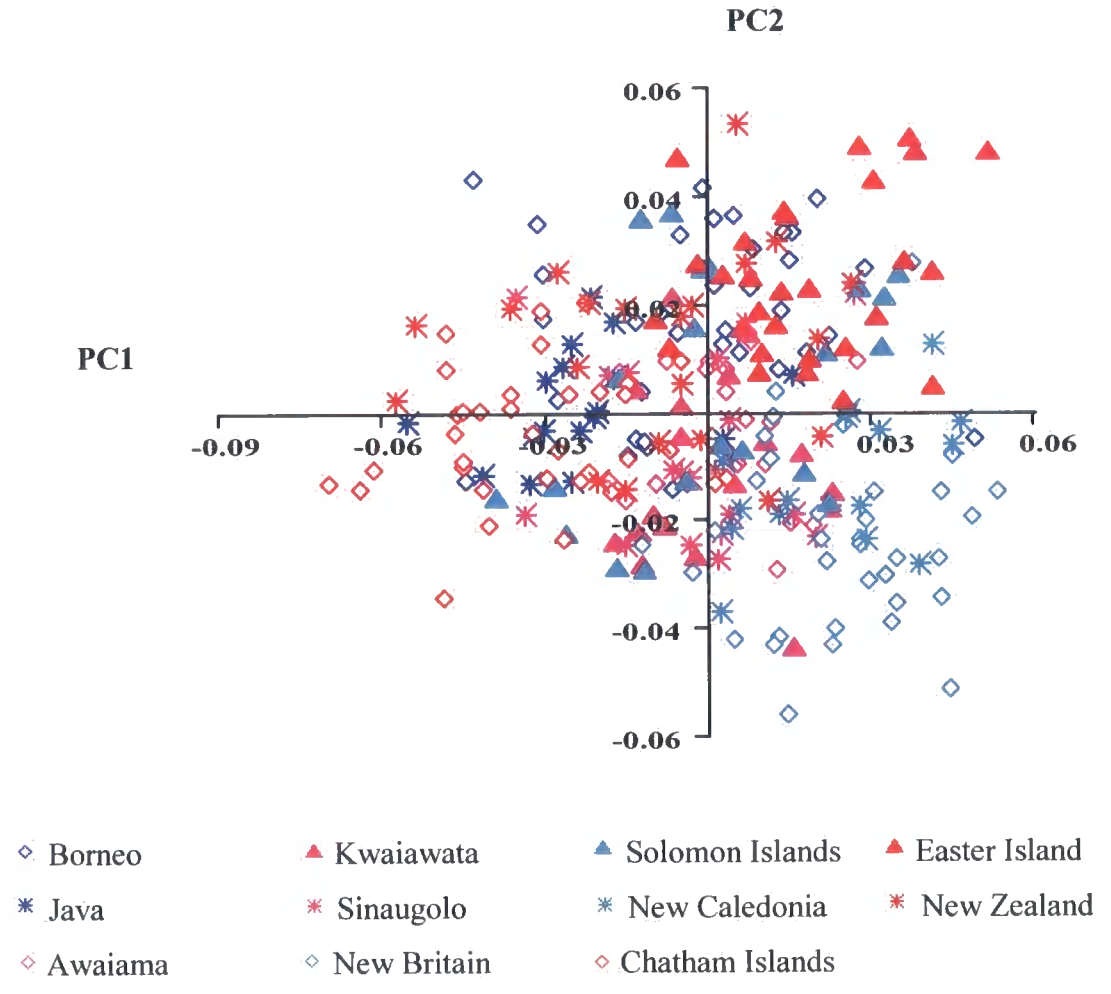


Table 7.2 Polynesia: The proportion of and accumulated variance of PCs 1 – 134, which account for almost 100% of total sample variance

PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %	PC	Prop. %	Cuml. %
1	12.50	12.50	**35**	0.65	82.70	**69**	0.20	95.19	**103**	0.06	99.06
2	9.07	21.57	**36**	0.60	83.29	**70**	0.19	95.38	**104**	0.06	99.12
3	7.36	28.93	**37**	0.59	83.88	**71**	0.18	95.56	**105**	0.05	99.17
4	5.29	34.22	**38**	0.58	84.46	**72**	0.18	95.74	**106**	0.05	99.22
5	4.26	38.48	**39**	0.54	85.00	**73**	0.18	95.92	**107**	0.05	99.27
6	3.83	42.31	**40**	0.52	85.52	**74**	0.17	96.09	**108**	0.05	99.32
7	3.35	45.66	**41**	0.50	86.02	**75**	0.17	96.25	**109**	0.05	99.36
8	3.18	48.84	**42**	0.48	86.50	**76**	0.16	96.41	**110**	0.04	99.41
9	2.83	51.67	**43**	0.48	86.98	**77**	0.15	96.56	**111**	0.04	99.45
10	2.52	54.19	**44**	0.47	87.45	**78**	0.15	96.71	**112**	0.04	99.49
11	2.51	56.70	**45**	0.44	87.89	**79**	0.14	96.85	**113**	0.04	99.53
12	2.04	58.74	**46**	0.43	88.32	**80**	0.14	96.99	**114**	0.04	99.56
13	1.72	60.46	**47**	0.42	88.74	**81**	0.13	97.12	**115**	0.03	99.60
14	1.63	62.09	**48**	0.41	89.15	**82**	0.13	97.25	**116**	0.03	99.63
15	1.58	63.67	**49**	0.40	89.55	**83**	0.13	97.38	**117**	0.03	99.66
16	1.48	65.15	**50**	0.38	89.93	**84**	0.12	97.50	**118**	0.03	99.69
17	1.42	66.57	**51**	0.37	90.29	**85**	0.11	97.61	**119**	0.03	99.72
18	1.32	67.89	**52**	0.34	90.63	**86**	0.11	97.72	**120**	0.03	99.74
19	1.19	69.08	**53**	0.34	90.97	**87**	0.11	97.83	**121**	0.03	99.77
20	1.14	70.22	**54**	0.33	91.30	**88**	0.10	97.93	**122**	0.02	99.79
21	1.07	71.29	**55**	0.32	91.61	**89**	0.10	98.03	**123**	0.02	99.81
22	1.01	72.30	**56**	0.30	91.91	**90**	0.10	98.12	**124**	0.02	99.83
23	1.00	73.30	**57**	0.30	92.21	**91**	0.09	98.21	**125**	0.02	99.85
24	0.96	74.26	**58**	0.29	92.50	**92**	0.09	98.30	**126**	0.02	99.87
25	0.95	75.21	**59**	0.28	92.78	**93**	0.08	98.38	**127**	0.02	99.89
26	0.88	76.09	**60**	0.28	93.06	**94**	0.08	98.46	**128**	0.02	99.90
27	0.84	76.94	**61**	0.27	93.32	**95**	0.08	98.54	**129**	0.01	99.92
28	0.79	77.73	**62**	0.26	93.59	**96**	0.08	98.62	**130**	0.01	99.93
29	0.76	78.49	**63**	0.26	93.84	**97**	0.07	98.69	**131**	0.01	99.94
30	0.75	79.25	**64**	0.25	94.09	**98**	0.07	98.76	**132**	0.01	99.95
31	0.74	79.99	**65**	0.24	94.32	**99**	0.06	98.83	**133**	0.01	99.96
32	0.71	80.70	**66**	0.23	94.55	**100**	0.06	98.89	**134**	0.01	99.97
33	0.70	81.40	**67**	0.22	94.77	**101**	0.06	98.95			
34	0.65	82.05	**68**	0.21	94.98	**102**	0.06	99.01			

Table 7.3 Polynesia: Cross validation study to assess the separation by proportion of sample variance

Sample	70% (PCs 1-20)	80% (PCs 1-31)	90% (PCs 1-50)	95% (PCs 1-68)	100% (PCs 1-134)
Bor	62.86%	60.00%	60.00%	54.29%	57.14%
Java	52.94%	58.82%	58.82%	70.59%	58.82%
ANG	63.16%	57.89%	57.89%	57.89%	47.37%
KNG	39.89%	44.44%	38.89%	50.00%	27.78%
SNG	28.57%	33.33%	61.90%	61.90%	57.14%
NB	74.29%	74.29%	74.29%	80.00%	68.57%
SI	47.62%	52.33%	61.90%	66.67%	38.10%
NC	33.33%	33.33%	53.33%	60.00%	46.67%
CI	100.00%	97.14%	97.14%	97.14%	88.57%
EI	100.00%	96.55%	93.10%	93.10%	96.55%
NZ	57.14%	57.14%	61.90%	61.90%	52.38%
Mean	**59.89%**	**60.48%**	**65.38%**	**68.50%**	**58.10%**

Table 7.4 gives the Mahalanobis distances between each of the samples. The largest distance is found between the Chatham Island and New Britain samples (D = 86.51). The smallest distance is found between the Borneo and Kwaiata (New Guinea) samples (D = 17.23). All distances are significant at $p \leq 0.05$.

Table 7.4 Mahalanobis' D distance matrix: Polynesia . * significant at $p < 0.05$.

Bor; Borneo; Java, Java; ANG, Awaiawama (New Guinea); KNG, Kwaiawama (New Guinea); SNG, Sinaugolo (New Guinea); NB, New Britain; SI, Solomon Islands; NC, New Caledonia; CI, Chatham Islands; EI, Easter Island; NZ, New Zealand.

	Bor	Java	ANG	KNG	SNG	NB	SI	NC	CI	EI	NZ
Bor	0.0000										
Java	17.52*	0.0000									
ANG	25.75*	36.83*	0.0000								
KNG	17.23*	25.98*	29.41*	0.0000							
SNG	22.10*	30.57*	22.35*	19.97*	0.0000						
NB	39.94*	54.35*	43.96*	29.48*	39.22*	0.0000					
SI	25.47*	38.81*	32.47*	23.53*	26.77*	24.11*	0.0000				
NC	41.18*	52.74*	41.81*	31.23*	39.22*	19.70*	33.75*	0.0000			
CI	62.52*	59.29*	77.81*	61.16*	52.42*	86.51*	46.55*	85.40*	0.0000		
EI	43.48*	54.07*	50.12*	44.92*	36.33*	57.87*	33.60*	49.76*	53.47*	0.0000	
NZ	37.57*	38.38*	47.11*	42.59*	32.10*	66.86*	40.71*	59.42*	37.51*	32.14*	0.0000

Table 7.5 Cross validation analysis: Polynesia

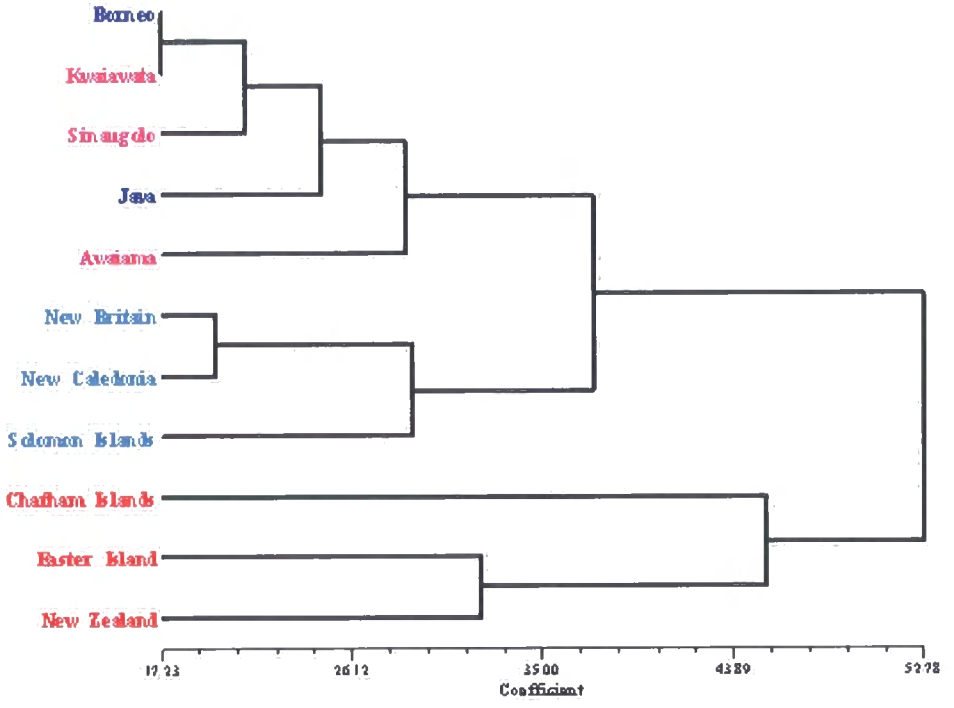
Bor; Borneo; Java, Java; ANG, Awaiawama (New Guinea); KNG, Kwaiawama (New Guinea); SNG, Sinaugolo (New Guinea); NB, New Britain; SI, Solomon Islands; NC, New Caledonia; CI, Chatham, Islands; EI, Easter Island; NZ, New Zealand.

	Bor	Java	ANG	KNG	SNG	NB	SI	NC	CI	EI	NZ	Total
Bor	**54.29**	8.57	2.86	17.14	2.86	2.86	5.71	2.86	0.00	2.86	0.00	100.00
Java	23.53	**70.59**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.88	100.00
ANG	15.79	0.00	**57.89**	10.53	15.79	0.00	0.00	0.00	0.00	0.00	0.00	100.00
KNG	16.67	5.56	0.00	**50.00**	16.67	0.00	5.56	5.56	0.00	0.00	0.00	100.00
SNG	0.00	0.00	9.52	4.76	**61.90**	0.00	23.81	0.00	0.00	0.00	0.00	100.00
NB	2.86	0.00	2.86	0.00	0.00	**80.00**	2.86	11.43	0.00	0.00	0.00	100.00
SI	4.76	0.00	0.00	14.29	0.00	4.76	**66.67**	0.00	4.76	0.00	4.76	100.00
NC	0.00	0.00	0.00	6.67	0.00	20.00	6.67	**60.00**	0.00	0.00	6.67	100.00
CI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**97.14**	0.00	2.86	100.00
EI	0.00	0.00	0.00	0.00	3.45	0.00	0.00	3.45	0.00	**93.10**	0.00	100.00
NZ	4.76	4.76	0.00	0.00	14.29	0.00	0.00	0.00	4.76	9.52	**61.90**	100.00

Table 7.5 gives the results of the cross validation analysis. The mean number of correctly placed individuals from all samples is 68.50% and all samples achieve 50% or more correct classification. The sample with the smallest percentage of correct classification is the Kwaiawata (New Guinea) sample, with only half of the individuals being accurately placed into their original group. The misclassified individuals are placed in either alternate Melanesian samples or with the Borneo sample. The sample with the highest percentage of correct classification is the Chatham Island sample, achieving 97.14%. The misidentified individuals from this sample are placed only in the New Zealand sample. The Easter Island sample also achieves a very high percentage of correctly classified individuals, with 93.10%. There is no significant correlation between the number of individuals in the sample and the percentage of correct classification.

Figure 7.3 illustrates the phenogram produced from the Mahalanobis D' distances between the samples. Three clear clusters are evident in this phenogram, with the first bifurcation containing the three Polynesian samples. Within this bifurcation the sample from the Chatham Islands is placed at a greater distance from those of New Zealand and Easter Island. A second cluster contains the Island Melanesian samples and the third those from New Guinea and Southeast Asia.

Figure 7.3 Phenogram illustrating distances between the Island Southeast Asian, Melanesian and Polynesian samples.



7.4.2 Craniofacial diversity in Melanesia and Polynesia: Means

The means of the samples analysed in section 7.4.1 are submitted to Procrustes fitting and principal components analysis, with the addition of a number of samples too small to be included in the full dataset analysis. From Island Southeast Asia the additional sample means include Moluccas, Sumatra, Timor and Sulawesi. From Melanesia the Loyalty Islands and Louisiade Archipelago samples are added and from Polynesia a Hawaiian sample is included. The percentage of variance explained by each PC is given in table 7.6. The results of PC1 (31.6%) versus PC2 (19.2%) are illustrated in figure 7.4. The Chatham Islands sample is separated from the remaining samples along PC3 (11.3%), as illustrated in figure 7.5. No single further PC or combination of PCs produces clear separation of the samples and the Polynesian samples do not cluster together on any of the PCs.

Figure 7.4. Melanesia and Polynesia means: PC1 v PC2

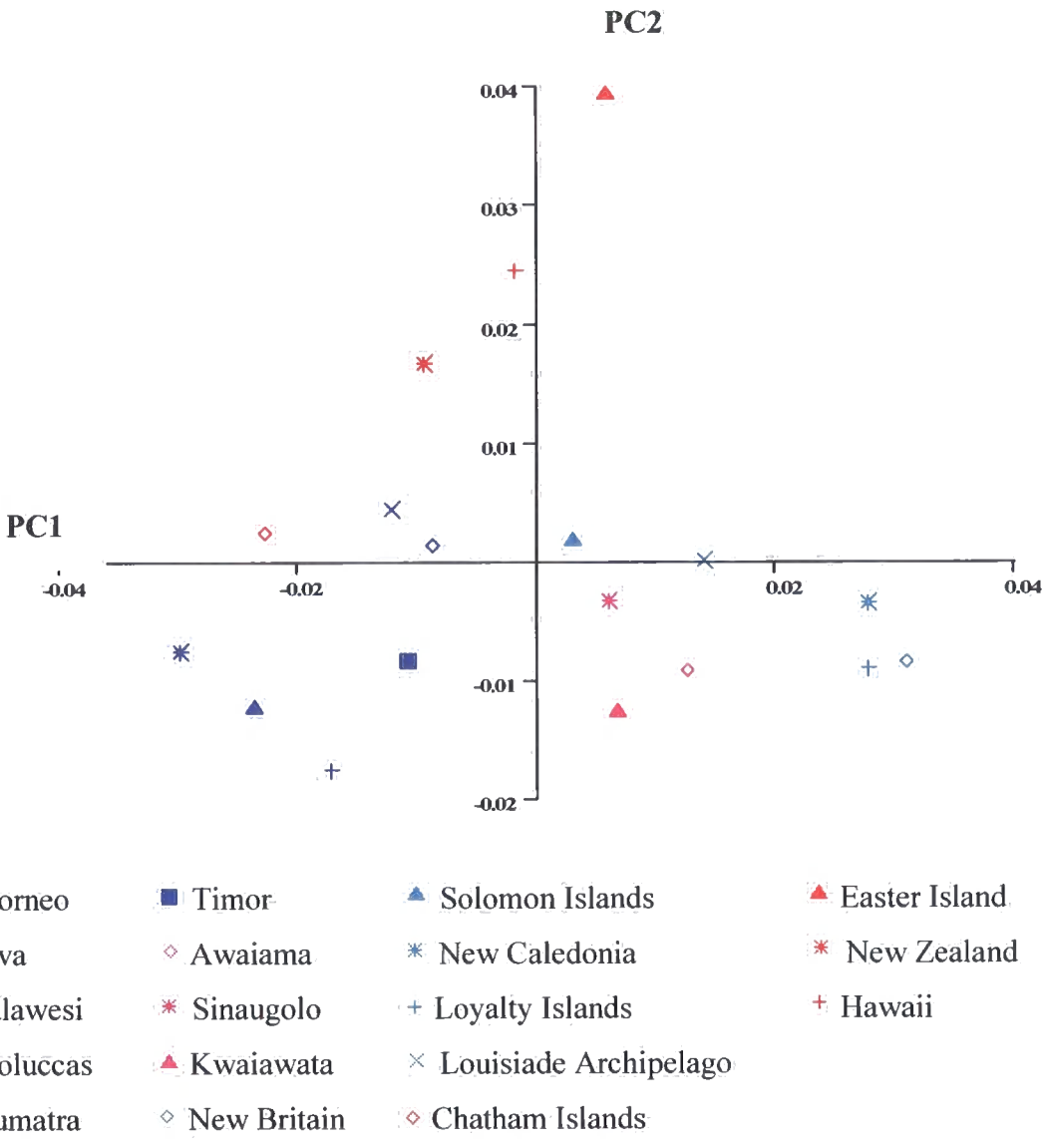
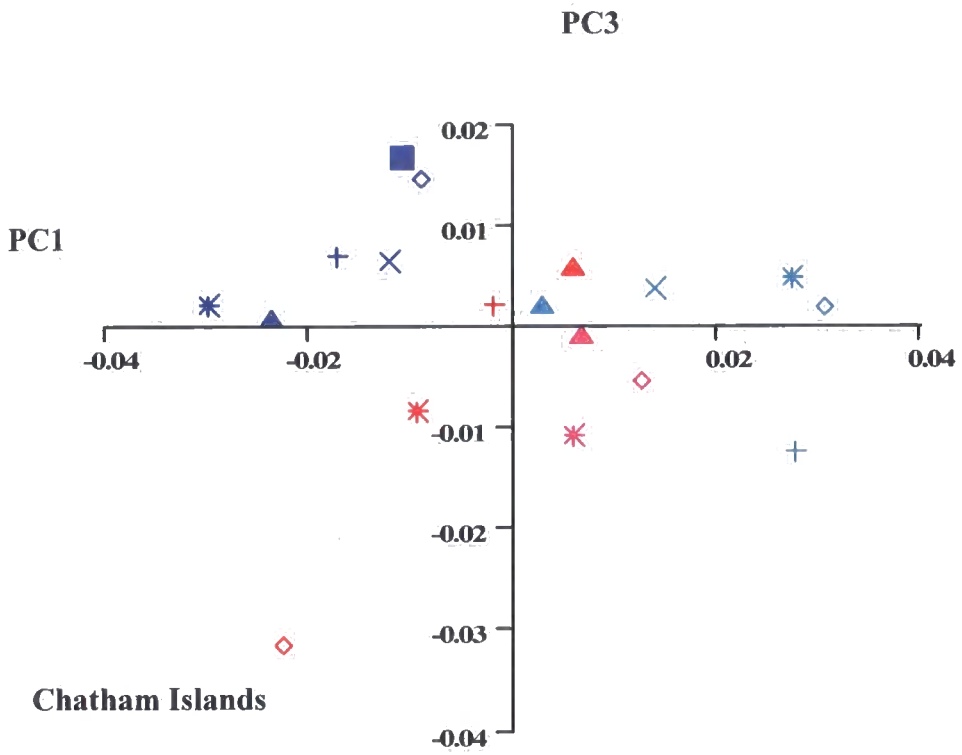


Figure 7.5. Melanesia and Polynesia means: PC 1 v PC 3



◇ Borneo	■ Timor	▲ Solomon Islands	▲ Easter Island
▲ Java	◇ Awaiama	✳ New Caledonia	✳ New Zealand
✳ Sulawesi	✳ Sinaugolo	+ Loyalty Islands	+ Hawaii
+ Moluccas	▲ Kwaiawata	× Louisiade Archipelago	
× Sumatra	◇ New Britain	◇ Chatham Islands	

Table 7.6 Southeast Asia, Melanesia and Polynesia means: The proportion and accumulated variance of PCs 1 – 17, which account for 100% of total sample variance

Principal Component	Variance %	Cumulative Variance %
1	31.6	31.6
2	19.2	50.8
3	11.3	62.1
4	8.4	70.5
5	6.1	76.6
6	3.8	80.4
7	3.2	83.6
8	2.6	86.2
9	2.5	88.7
10	2.2	90.9
11	1.7	92.6
12	1.7	94.3
13	1.4	95.7
14	1.3	97.0
15	1.2	98.2
16	1.0	99.2
17	0.8	100.0

The mean configurations at the negative and positive extremes of PC1 are illustrated in figure 7.6. At the negative extreme the craniofacial shape is characterised by a relatively posteriorly sloping face (figure 7.6 i) with glabella situated relatively posteriorly (figure 7.6 ii). As the shape is warped to the positive extreme of PC1 the face decreases in relative height (figure 7.6 iii), with the palate and maxilla becoming relatively more superiorly and anteriorly positioned (figure 7.6 iv). Glabella is situated relatively more anteriorly at the positive extreme of PC1 (figure 7.6 v) and the basicranium is relatively lengthened (figure 7.6 vi).

The changes identified along PC2 are defined by the separation of the Easter Island sample, and to a lesser extent the Chatham Islands and Hawaii samples, from the remaining sample means (figure 7.7). The mean configuration at the negative extreme of PC1 is characterised by a pronounced posteriorly sloping face (figure 7.7 i) with a relatively posterior placement of glabella (figure 7.7 ii) and a relatively anteriorly situated maxilla (figure 7.7 iii). Towards the positive extreme, where the Easter Island sample is situated, the relative slope of the face has decreased (figure 7.7 iv). Glabella and the upper face are relatively more anteriorly placed (figure 7.7 v), whilst the palate and zygomatic are relatively more superiorly situated (figure 7.7 vi). Stephanion is relatively more inferiorly and anteriorly placed towards the positive extreme of PC2 (figure 7.7 vii).

The Chatham Islands sample is separated from all other samples along PC3. Figure 7.8 illustrates the differences between the Chatham Islands sample, situated towards the negative extreme of PC3, and all other samples placed towards the positive extreme. The Chatham Island sample, represented by the lower figure, is characterised by a relatively low and long forehead (figure 7.8 i). A relatively deep maxilla is displayed (figure 7.8 ii) in comparison to the remaining samples (figure 7.8 iii), and the maxilla is relatively posteriorly situated at the negative extreme of PC3 (figure 7.8 iv). The Chatham Islands sample also displays a relatively inferiorly and anteriorly placed inion (figure 7.8 v), with a relatively more compact basicranium (figure 7.8 vi) and relatively more posteriorly and laterally situated zygomatics (figure 7.8 vii).

Figure 7.6 PC1 TPS: Differences in shape along the first PC. The upper figure represents the mean landmark configuration warped along PC1 from the negative to the positive extreme

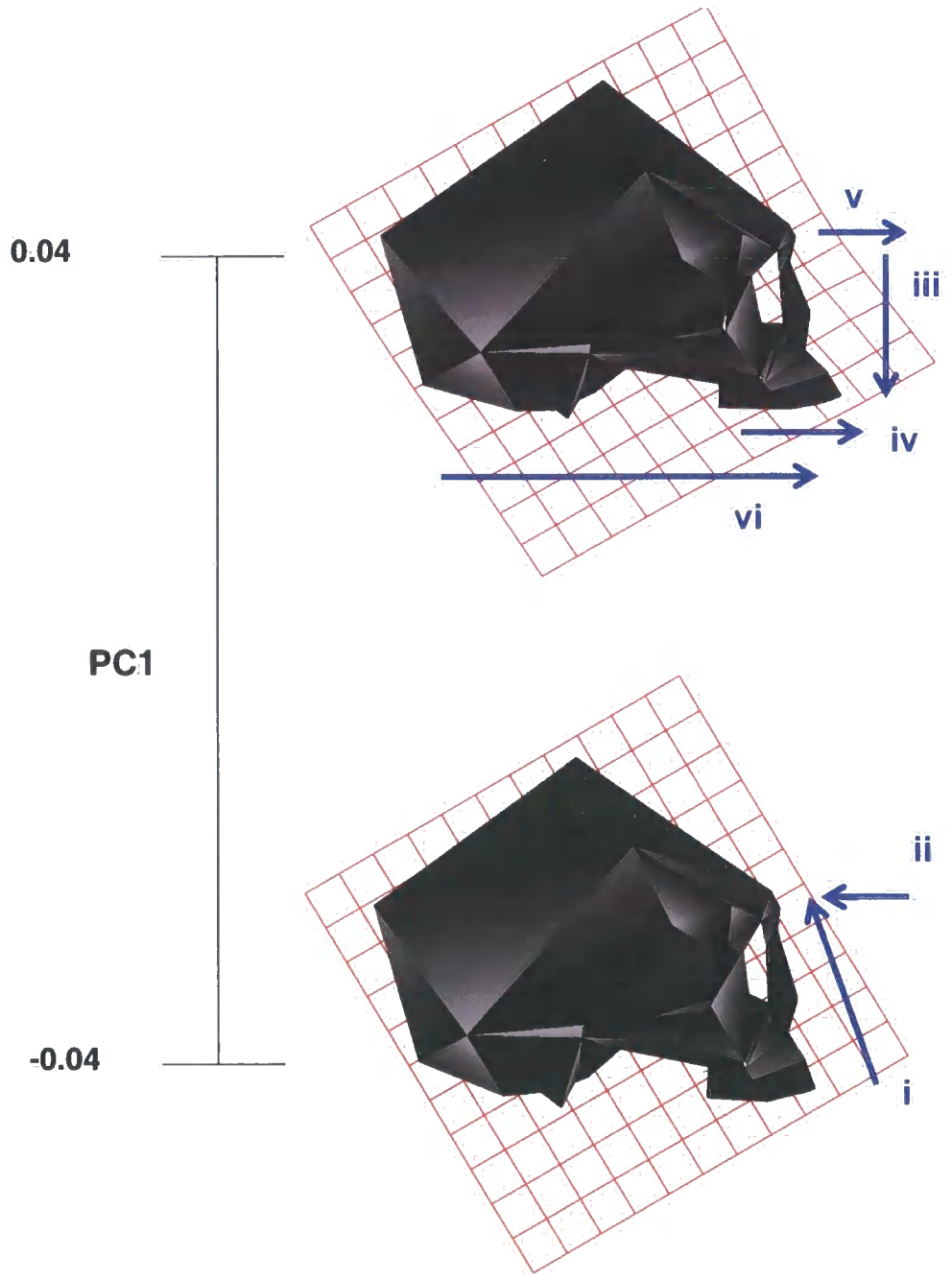


Figure 7.7 PC2 TPS: Differences in shape along the second PC. The upper figure represents the mean landmark configuration warped along PC2 from the negative to the positive extreme

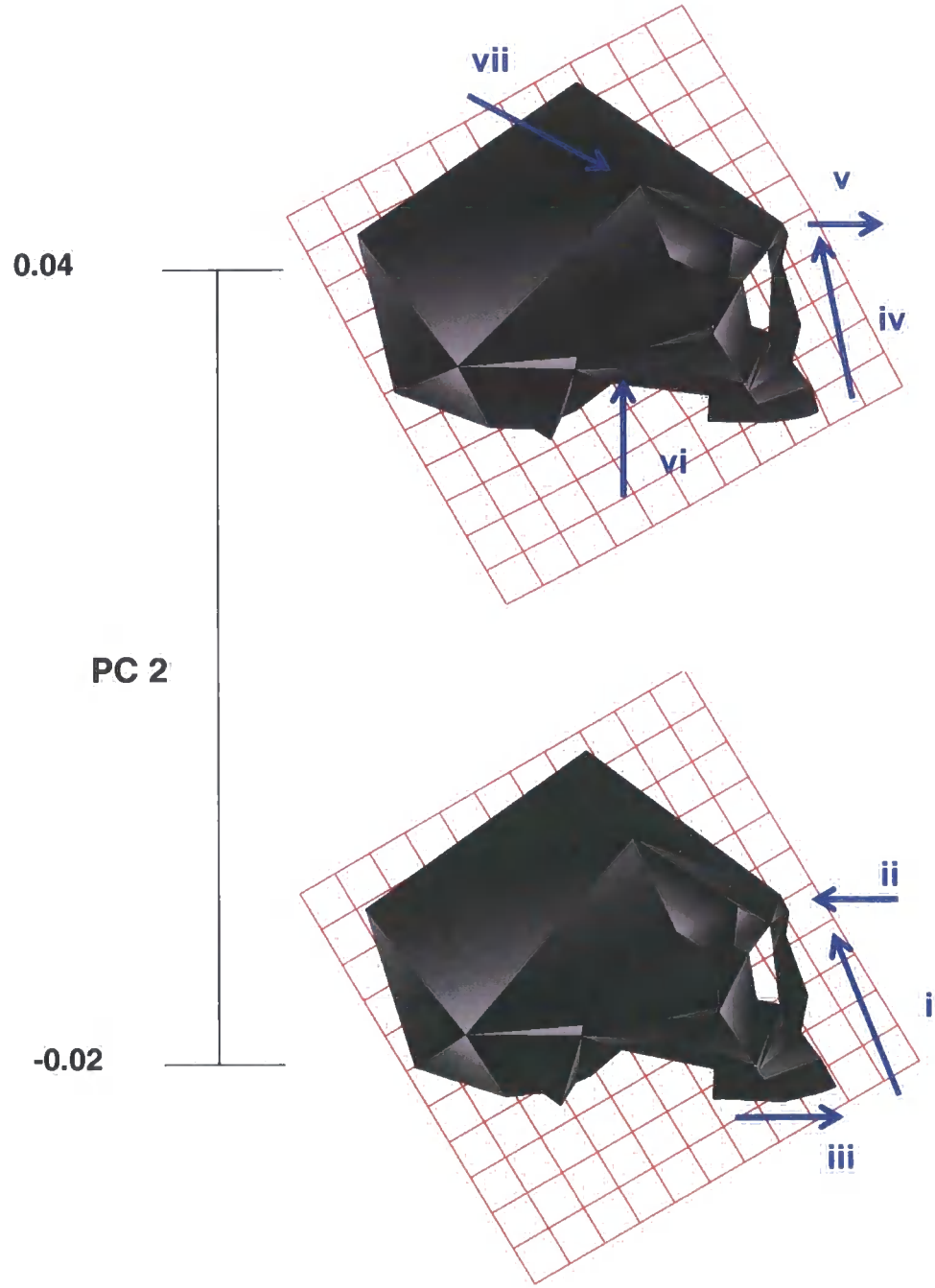


Figure 7.8 PC3 PC1 TPS: Differences in shape along the third PC. The upper figure represents the mean landmark configuration warped along PC3 from the negative to the positive extreme

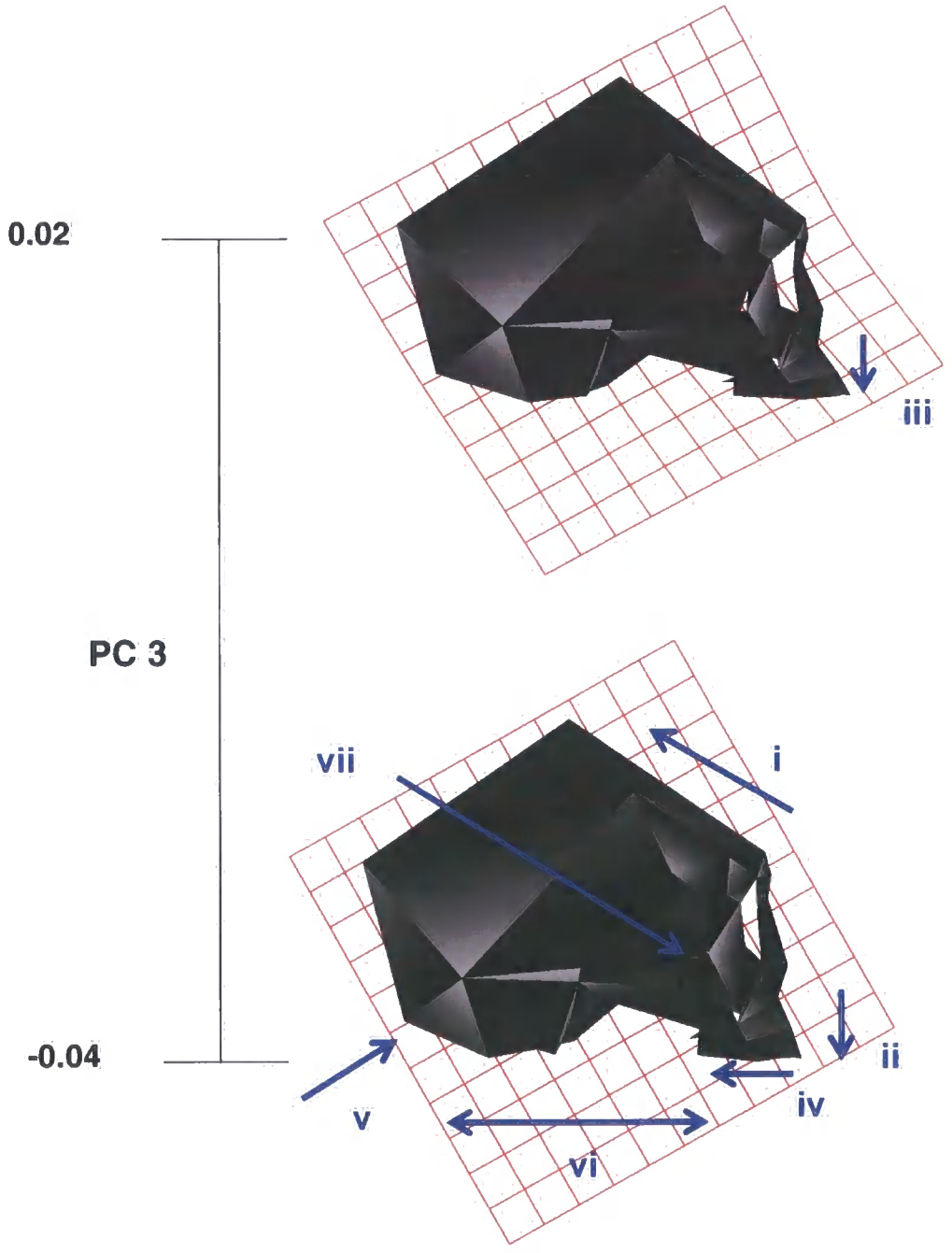
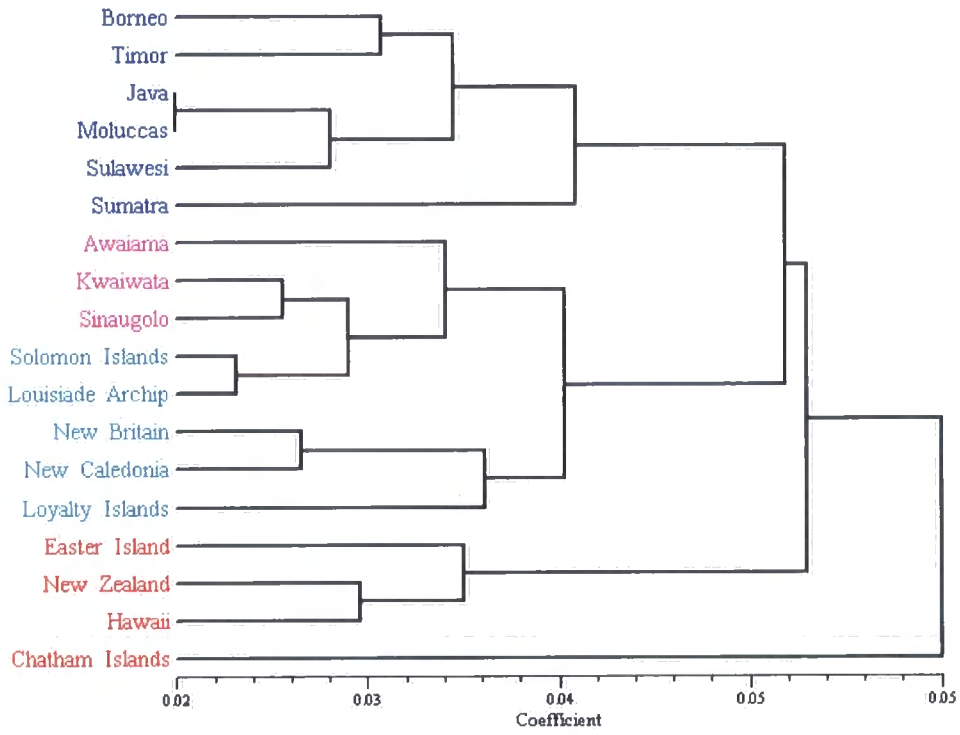


Figure 7.9 shows the phenogram produced from the Procrustes Distances (table 7.7) between the sample means. The first sample separated is the Chatham Islands, illustrating their distinct craniofacial morphology. The three remaining Polynesian samples are situated on the second bifurcation. All other samples fall into two clusters, one containing all Island Southeast Asia samples and the other the New Guinea and Melanesian samples.

Figure 7.9 Phenogram illustrating distances between the Island Southeast Asian, Melanesia and Polynesian samples.



A correlation between the Procrustes distances (table 7.7) and geographic distances (table 7.8), calculated from the distance between the latitude and longitudinal coordinates of the samples, produced a strong and highly significant correlation ($r = 0.42$, $p < 0.001$).

Table 7.7 Procrustes distance matrix: Island Southeast Asia, Melanesia and Polynesia

	Bor	Java	Sul	Mol	Sum	Tim	Awai	Kwai	Sin	NB	SI	NC	LA	LI	CI	EI	NZ	Haw
Bor	0.0000																	
Java	0.0359	0.0000																
Sul	0.0387	0.0283	0.0000															
Mol	0.0357	0.0250	0.0332	0.0000														
Sum	0.0363	0.0409	0.0415	0.0406	0.0000													
Tim	0.0326	0.0336	0.0352	0.0329	0.0398	0.0000												
Awai	0.0418	0.0459	0.0551	0.0478	0.0531	0.0490	0.0000											
Kwai	0.0355	0.0371	0.0458	0.0373	0.0439	0.0368	0.0330	0.0000										
Sin	0.0399	0.0399	0.0455	0.0416	0.0461	0.0421	0.0307	0.0290	0.0000									
NB	0.0526	0.0607	0.0662	0.0547	0.0564	0.0519	0.0461	0.0371	0.0412	0.0000								
SI	0.0288	0.0405	0.0426	0.0396	0.0327	0.0341	0.0382	0.0305	0.0299	0.0393	0.0000							
NC	0.0483	0.0579	0.0624	0.0538	0.0554	0.0482	0.0416	0.0351	0.0402	0.0296	0.0396	0.0000						
LA	0.0368	0.0494	0.0527	0.0482	0.0401	0.0419	0.0380	0.0312	0.0339	0.0387	0.0273	0.0363	0.0000					
LI	0.0546	0.0599	0.0652	0.0564	0.0527	0.0544	0.0413	0.0397	0.0381	0.0355	0.0395	0.0375	0.0375	0.0000				
CI	0.0538	0.0439	0.0436	0.0505	0.0491	0.0548	0.0596	0.0502	0.0470	0.0672	0.0471	0.0658	0.0562	0.0616	0.0000			
EI	0.0496	0.0619	0.0626	0.0641	0.0538	0.0567	0.0583	0.0559	0.0502	0.0591	0.0461	0.0530	0.0502	0.0624	0.0638	0.0000		
NZ	0.0367	0.0402	0.0439	0.0445	0.0436	0.0447	0.0442	0.0431	0.0359	0.0561	0.0360	0.0516	0.0460	0.0542	0.0426	0.0391	0.0000	
Haw	0.0370	0.0484	0.0492	0.0509	0.0370	0.0441	0.0492	0.0453	0.0402	0.0532	0.0335	0.0494	0.0381	0.0521	0.0506	0.0323	0.0318	0.0000

Table 7.8 Minimum distances between samples calculated from longitude and latitude coordinates (km)

Bor	0																	
Java	944	0																
Sul	1,180	1,222	0															
Mol	21,483	2,149	1,018	0														
Sum	945	1,210	2,048	3,067	0													
Tim	2,009	1,623	939	834	2,739	0												
Awai	4,639	4,429	3,461	2,463	5,489	2,809	0											
Kwai	4,756	4,582	3,582	2,574	5,620	2,966	212	0										
Sin	4,262	4,060	3,084	2,087	5,112	2,442	377	526	0									
NB	4,638	4,638	3,551	2,534	5,598	3,061	693	524	804	0								
SI	5,631	5,462	4,461	3,449	6,502	3,843	1,037	883	1,402	1,402	0							
NC	6,632	6,234	5,462	4,525	7,395	4,658	2,159	2,145	2,500	2,527	1,586	0						
LA	4,928	4,704	3,749	2,754	5,774	3,082	292	279	667	781	785	1,885	0					
LI	6,674	6,301	5,500	4,549	7,452	4,713	2,149	2,119	2,501	2,474	1,502	166	1,867	0				
CI	8,790	8,123	7,200	6,463	8,774	6,273	4,903	4,939	5,184	5,371	4,453	2,868	4,275	2,686	0			
EI	14,927	14,308	13,794	12,889	15,514	12,916	10,480	10,414	10,842	10,635	9,606	8,365	10,190	8,347	6,185	0		
NZ	8,021	7,369	6,953	6,190	8,577	6,031	4,182	4,233	4,447	4,688	3,820	2,245	3,955	2,358	775	6,940	0	
Haw	10,136	10,471	9,253	8,359	11,062	9,076	6,630	6,422	6,900	6,130	5,726	6,187	785	1,502	8,088	7,488	7,484	0
	Bor	**Java**	**Sul**	**Mol**	**Sum**	**Tim**	**Awai**	**Kwai**	**Sin**	**NB**	**SI**	**NC**	**LA**	**LI**	**CI**	**EI**	**NZ**	**Haw**

7.5 Discussion

7.5.1 Craniofacial diversity in Melanesia and Polynesia

Polynesia was one of the last areas of the world to be settled by *Homo sapiens*. This settlement took place rapidly, over a period of about 3,000 years, and during this time a distinct craniofacial morphology emerged (Houghton, 1996). In order to assess the biological affinities and possible origins of the Polynesians, this chapter analysed samples from Island Southeast Asia, Melanesia and Polynesia. Among the samples assessed were some of the most isolated human populations, including the Chatham Islands and Easter Island. These islands are geographically isolated and following initial settlement some of the islands remained free from outside interaction until European contact many centuries later.

Conflicting results are obtained in regard to Polynesian morphological affinity from the full dataset analyses and those using the sample means. The analyses of the full dataset appear to show that the Polynesian samples are on the whole morphologically distinct from the New Guinean, Melanesian and Southeast Asian samples. The Mahalanobis' distances between all the samples, for example, are statistically significant (table 7.4). Similarly the cross validation analysis produced a high overall percentage of correctly classified individuals at 68.5%. At least half of all individuals in each sample were correctly placed in their original groups and two of the Polynesian samples achieved over 90% correct classification (table 7.5). Additionally the phenogram created from the Mahalanobis' distances distinguishes the three Polynesian samples from all remaining samples, separating them at the first bifurcation (figure 7.3). The phenogram further clusters the Island Southeast Asian and the New Guinea samples together, whilst the three Melanesian samples group on a separate branch (figure 7.3). These results suggest strong dissimilarities between the craniofacial shape of the different regions, with the Polynesians in particular being the most morphologically distinct. Hypothesis $\mathbf{H_1}$ stated that the populations of Polynesia are not morphologically distinct from those of Southeast Asia and Melanesia. The results from the analyses of full dataset indicate that the Polynesian samples are distinct in craniofacial shape from the Melanesian and Southeast Asian samples and therefore the null hypothesis, $\mathbf{H_1}$, is refuted.

The results of the principal components analysis of the sample means, however, do not give such a strong morphologically distinct signal as that seen with the full data set (figure 7.3). The four Polynesian samples do not form a separate cluster on the principal components graph, rather they are spread along the length of PC2, with the Easter Island sample situated at the positive extreme (figure 7.4). Along PC1, the Polynesian samples are positioned at the negative extreme, along with the Island Southeast Asian samples (figure 7.4). The New Guinean and Melanesian samples are clustered toward the positive extreme of PC1, suggesting that the differences in morphology described by this PC are driven by the differences between the Southeast Asian and Polynesian samples on one hand, and the New Guinean and Melanesian samples on the other (figure 7.4). Along PC1 the Chatham Islands sample falls within the morphological range of the Southeast Asian samples (figure 7.4). The Chatham Islands sample, however, is separated from all other samples by the variance described by PC3 (figure 7.5). The distinctiveness of this sample is further illustrated in the phenogram, created from the Procrustes distances between the sample means (figure 7.9). The first bifurcation of the phenogram separates the Chatham Islands sample from all others (figure 7.9). The second bifurcation contains the remaining Polynesian samples, including the additional sample from Hawaii. The Island Southeast Asian samples and the New Guinea/Melanesian samples are placed within two separate clusters. This finding emphasises the distinctive craniofacial morphology of the Polynesian samples from that of the Melanesian and Southeast Asian samples in this study. The separation of the Polynesian samples along PC2 (figure 7.4) further suggests that whilst the Polynesians are a homogenous group when compared with other Oceanic populations, as suggested by Houghton (1996), there is in fact differentiation between them. The differences along PC2 are largely driven by the distinctiveness of the Easter Island sample (figure 7.4). Genetic evidence from the Pacific rat (*Rattus exulans*), used as a proxy for human settlement, suggests that there was only a single or limited introduction of the animal to Easter Island (Barnes *et al.*, 2006). The limited mtDNA of the Easter Island rats points to extreme isolation of Easter Island, suggesting that the human population also remained isolated following initial settlement (Barnes *et al.*, 2006). A

similar situation is revealed for the Chatham Islanders, with a single founding event followed by isolation (Matisoo-Smith *et al.*, 1998). The Chatham Islands sample displays even greater disparity from the other Polynesian samples (figures 7.5 and 7.9), even though they were separated from their founding population for a relatively short period. Isolation is therefore interpreted as a major factor in creating the distinct morphology found in the Easter Island and Chatham Islands sample in the present study. Lum *et al.* (2002) suggested that gene flow was primarily focused among neighbouring populations as indicated by the robust correlation between genetic and geographic distances between Polynesian populations. To confirm any similar effects identifiable in the craniofacial morphology of the Polynesians, a correlation between Procrustes distances and geographic distances was undertaken. A strong and significant correlation was found, illustrating that within populations only separated by a relatively short period of time, isolation by distance plays an important role in creating the observed morphological diversity.

Previous craniometric studies have found a distinction between samples from New Guinea and Melanesia on the one hand, and those from Polynesia on the other (Pietrusewsky and Chang, 2003). Pietrusewsky and Chang (2003) interpret their findings as showing an early colonisation of Australia and Near Oceania by a group of people morphologically distinct from those who now occupy Polynesia. This is echoed by the results of this chapter and can be interpreted as providing no evidence for an ancestral Polynesian homeland in Melanesia, as suggested by the Entangled Bank model (Terrell *et al.*, 2001). The results of the present study indicate a clear distinction between the New Guinea/Melanesian samples and those from Polynesia. Pietrusewsky and Chang (2003) further suggest morphological similarity between Southeast Asian and Polynesian samples, interpreted as supporting an ancestral Polynesian homeland in Island Southeast Asia. This finding is not fully supported by the results of this chapter. Although the PCA of the sample means detected some similarity in craniofacial shape along PC1, the overall results of this chapter demonstrate that the Polynesians are morphologically distinct and homogeneous in relation to samples from neighbouring regions. This is not to say that the Polynesians may not have had a common ancestor

with the Island Southeast Asian populations. It has been suggested that genetically at least, extant Polynesians share many features with contemporary Island Southeast Asians, but have undergone further, rapid evolution over the last 3,000 years (Serjeantson and Gao, 1995). Some similarity is indicated with Southeast Asian morphology and the present distinctiveness of the Polynesians could also be the result of rapid microevolution. The results of this chapter therefore do not support a direct link with Island Southeast Asians but do not rule out completely a shared ancestral population. Evolution due to founder effects, local adaptation and gene flow within small and isolated populations may have brought about the morphological differences now found between Polynesians and Southeast Asians. Pietrusewsky (1988, 1992) has demonstrated a likely connection between Neolithic populations of Southeast Asia and Polynesia. It may be possible to address this issue in more detail by including pre-Neolithic specimens from Island Southeast Asia in future analyses. Comparing specimens from before and after any possible secondary migrations in Island Southeast Asia should enable a more accurate assessment of any Polynesian ancestry in the region.

The craniofacial distinctiveness of the Polynesians is all the more surprising given the relatively short period of time in which the diversification has developed. Although not confirming a possible founding population for the Polynesians, the results of the analyses here give support to the assumption that rapid local evolution has created a distinct craniofacial morphology for the Polynesians. Although having only been settled for a short period of time in relation to the occupation of Melanesia, the Polynesian islands have produced samples that are distinct from their potential ancestral homelands. This observed distinction in morphology is most likely related to the reduced diversity in Polynesians that has been reported for many genetic markers (Kayser *et al.*, 2000). This reduction of genetic diversity has been taken as indicating a series of bottlenecks in the Polynesians (Lum *et al.*, 2002). The bottlenecks will have played a role in creating diverse morphological groups distinct from their founding population. As a group, the Polynesian samples are fairly heterogeneous, with large biological distances between them (table 7.4). This finding is contrary to other morphological descriptions, where Polynesian morphology has been described as relatively homogeneous (Houghton,

1996). A particular distinction is evident between the sample from the Chatham Islands and the remaining Polynesian samples (figures 7.5 and 7.9). This is surprising in terms of the known settlement pattern of these islands. The Chatham Islands are believed to have been occupied by a group from New Zealand and the most recent dates for the settlement of New Zealand suggest this happened at around the same time (Kirch, 2000; Wilmshurst and Higham, 2004). The morphological dissimilarity from their presumed parental population can therefore be attributed to a single founding event, evidenced by the mtDNA from the rats that travelled with the settlers (Kirch, 2000). As with Easter Island, the islands subsequently remained isolated until European contact allowing founder effect and gene flow within a small population to contribute to the morphological diversification. Isolation following the initial settlement would account for the perceived differences between the Polynesian samples in this study.

7.5.2 Summary of craniofacial diversity in Polynesia

Terrell (2004) stressed that the human colonisation of Polynesia was a social as well as a demographic phenomenon, happening in a world that was changing environmentally as well as culturally. He argues for a more involved story than simply having people migrating from point A to point Z. This view can be compared with the convoluted colonisation scenarios that result from the mtDNA and Y chromosome data (Ohashi *et al.*, 2004). Utilising all the differing data sources for the dispersal of the Polynesians creates a far more complex picture of settlement patterns. The morphological data defines a homogenous Polynesian grouping in relation to the possible founding populations, which does not reflect the admixture with the Melanesians evidenced by genetic analyses. This relative morphological homogeneity is most likely the product of the series of bottlenecks that the Polynesian ancestors underwent during the initial colonisation (Lum *et al.*, 2002). Diversification from this homogenous morphological grouping was then created by specific settlement patterns and demography of individual islands within Polynesia. This demonstrates that even when only a short period of isolation has occurred, founder effect, followed by isolation and genetic drift can significantly influence the craniofacial morphology of differing populations.

- Analyses of the full dataset demonstrate the morphological distinctiveness of the Polynesian samples

- Although overall distinct from the other samples, the Polynesian samples are not homogeneous as a group

- Diversification between the Polynesians is likely caused by a series of founder effects followed by isolation

- Isolation by distance is an important factor in creating the morphological diversity observed in the Polynesian samples

- The conflicting results suggesting possible similarities with the Island Southeast Asian samples may indicate an ancient shared ancestry from which the Polynesians have diversified

- The present study does not give clear support to any of the previously suggested models and would require the addition of samples from East Asia and the inclusion of prehistoric specimens to fully address this question.

Chapter 8

Summary and Conclusion

8.1 Summary of results

The overall aim of this study has been to explore the craniofacial diversity found in modern human populations around the Indian Ocean rim in relation to the initial dispersal of *Homo sapiens* into that region. This is done by looking at possible causes of morphological diversity in the craniofacial skeleton, including migration and epigenetic factors.

The first set of analyses undertaken (Chapter 3) states that although there is only a restricted amount of variation in the human craniofacial skeleton (Relethford, 1994), the samples from the Indian Ocean rim could be statistically discriminated from one another. Having thus determined that there is quantifiable variation between human populations from different geographic locations, subsequent analyses explore possible causal reasons for the patterns of morphological diversity found. The results of Chapter 3 also highlight that there is strong regional clustering of craniofacial shape in the sample populations, demonstrating a relationship between morphology and geography, which might in turn be charting migratory history. This is further substantiated by weak but significant correlations found between biological and geographic distances, using both minimum distance and estimated coastal routes between the localities. A strong correlation is found between geographic and biological distances from Africa, whilst a similar correlation of distances from Australia obtained a significant but weaker result. This is interpreted as providing explicit support for the proposed southern route out of Africa.

Having determined that geography and migration play, at least in part, a causal role in the patterns of craniofacial diversity found around the Indian Ocean rim, it is further demonstrated that epigenetic factors are also important in shaping the cranium (Chapter 4). Procrustes distances between the samples are found to be significantly correlated with both average high and low temperatures. As the Procrustes distances represent inter-sample differences in the overall shape of the

craniofacial skeleton, this demonstrates that the morphological variability between the sample populations is in part determined by environmental effects. Correlations are also found between environmental variables and specific aspects of inter-sample variance, as illustrated by individual principal component scores. Temperature is again important, correlating significantly with both PCs 1 and 3. As PC1 explains the greatest amount of variance in the sample, this is a likely cause for temperature alone being found to have an effect on the overall craniofacial shape. PC3 also correlates significantly with annual precipitation, as does the eighth principal component. PC8 further significantly correlates with the Primary Productivity Index (PPI), a seasonality index which reflects the length of the plant growing season. These combined findings are interpreted as showing that in addition to migratory history, craniofacial morphology is also partly determined by environmental factors such as temperature and rainfall. The significance of the PPI suggests that there may be a link between the significance of the climatic variables and diet. Diet and the role that it may play on the perceived craniofacial variation found around the Indian Ocean rim cannot, however, be directly tested in this study.

Present day patterns of craniofacial diversity around the Indian Ocean rim have been shown to be partly the result of the first migration out of Africa from a common ancestral population and partly through adaptation to local environments and potentially, diet. Strong regional clustering of morphologies is noted, with distinct differences between South and Southeast Asian samples on the one hand, and those from Melanesia and Australia on the other (Chapter 3). An additional region, Polynesia, is also considered which although not occupied as part of the proposed southern route out of Africa, provides an interesting comparison in that it was settled very rapidly from a single founding population. In most cases (Chapters 5 - 7) distinct intra-regional morphologies were apparent, as for example in the South and Southeast Asian samples. Although the patterns of craniofacial diversity at the regional levels were assessed in relation to specific models of origin, in most cases it was not possible to confirm or refute these models due to the composition of the present data set. The present data were specifically collected to explore evidence of the Late Pleistocene dispersal out of Africa. In order to fully answer the more specific questions, such as the number of founding populations for present day

Australian Aborigines, more geographic populations will need to be included in the analyses and, most importantly, relevant fossil data.

An important question relating to the proposed southern route migration is whether certain extant populations found within Southeast Asia represent 'relics' of this early dispersal out of Africa (Endicott *et al.*, 2003a). The Nicobar Islanders, the Andamanese and the Veddah of Sri Lanka have all been postulated at some time as being examples of such relic populations (Nei and Roychoudhury, 1993; Howells, 1993). The results of Chapter 5 demonstrate that the Veddah show a similar morphology to other Sri Lankan samples. The Nicobar and Andaman Islanders, on the other hand, have very distinct morphologies and do not show close similarities in craniofacial shape with their immediate geographic neighbours, including one another. No morphological similarity is found between any of the three proposed relic samples and two samples from Africa (Chapter 5). Although the Nicobar and Andaman Islanders are morphologically distinct it is not concluded that they represent relic populations from the Late Pleistocene dispersal from Africa. The distinct craniofacial morphology that these samples display is rather interpreted as being the result of long term isolation, particularly in the case of the Andaman Islanders, combined with founder effect and genetic drift.

The Melanesia and Australian region is considered in Chapter 6. A notable finding is that there is morphological similarity between samples from the islands of New Britain and New Caledonia, although they are relatively geographically distant within the region of Melanesia and are found on either side of the Near and Remote Oceanic divide. The three Australian samples included in the study display a similar morphology and always cluster together in the different sets of analyses. Having examined craniofacial morphology in detail in this region the conclusion is reached that the notion of an 'Australo-Melanesian' morphological complex frequently discussed in the literature (e.g. Bellwood, 1997; Pietrusewsky, 2006) must be rejected. The evidence from the present study suggests that although these samples may have once shared a common ancestral population, there is a complex pattern of diversity that cannot simply be considered under a single unifying label. This finding is echoed in the results of the analyses on Polynesian samples (Chapter 7). Here a homogenous morphology is interpreted for the Polynesians in relation to the

Melanesian and Southeast Asian samples, as is described by previous researchers (e.g. Houghton, 1996). Considerable diversity exists, however, between the Polynesian samples themselves. This diversity is interpreted as being the result of extreme isolation in the cases of the Chatham Islands and Easter Island samples, and serial founder effect as the widespread islands of Polynesia were settled. The observed craniofacial heterogeneity is interesting as it happened over a relatively short period of time. It highlights that morphological diversification from a common ancestral type can happen relatively rapidly and becomes fixed within a specific population.

8.2 Conclusions

8.2.1 Causes of craniofacial diversity

This study has examined craniofacial diversity around the Indian Ocean rim in relation to a dispersal out of Africa by a proposed southern route during the Late Pleistocene. Human dispersal can affect craniofacial diversity in various ways, some of which have been explored in the present study. Migration can affect diversity by isolating populations from one another so that distinct groups will diverge from a common ancestral morphological type. Gene flow, in this sense, is a fundamental evolutionary process. The effects of such isolation can be extreme when the populations involved have been completely isolated, such as is thought to have been the situation with people from the Andaman and Chatham Islands. The situation of the latter population, however, demonstrates that such isolation does not have to occur for a long period of time in order for diversification to occur. When humans disperse from one locality to another they can be exposed to novel environmental conditions that are different to those encountered before. Skeletal shape can thus be affected by adaptation to local environments, be this directly due to climatic variables, or due to the diet and biomechanical stressors relating to the environment.

That craniofacial diversity can come about by multiple small founder effects from a single ancestral population is seen explicitly on a micro-evolutionary level within Polynesia. It is likely that the dispersal along the proposed southern route may also have involved serial founder effects, which combined with local adaptation and gene flow, has created craniofacially diverse populations. Multiple dispersal events out of Africa, as suggested by Lahr and Foley (1994), do not need to be invoked in order to

explain the patterns of diversity that are found in extant populations occupying the Indian Ocean rim. Genetic studies, both mtDNA and Y chromosomal, support this by continuing to produce evidence for a single dispersal (Forster, 2004: Oppenheimer, 2003; Macaulay *et al.*, 2005; Thangaraj *et al.*, 2005), although this is not universally accepted (Smith *et al.*, 2007). Arguments against a single migration have stressed the substantial differences in stone tool industries between South Asia and Australia (Misra, 2005; Smith *et al.*, 2007). The lack of a clear industrial signal between the regions may, however, relate to the variety of adaptive responses that were undertaken by modern humans as they dispersed from South Asia to Australia (James and Petraglia, 2005). Thus a disruption in lithic technology can be seen to echo the disruption in morphology between the two regions but does not necessarily require separate ancestral populations. The disparity in craniofacial morphology seen in all the regional stages around the Indian Ocean rim has been created through a complex series of dispersals and evolutionary events.

A 'population sampling' model is proposed in which craniofacial diversity is created from a combination of multiple founder effects and local adaptation. A single dispersing population could have left Africa, with the process of diversification originating in gene flow and accentuated by adaptation to the local environment once in a new location. A 'sample' from this original diversified population would then disperse to a new locality and the process would begin again. Thus over time the original and the terminal populations would be craniofacially distinct from another. That morphological diversity can evolve through a combination of these proposed factors has wider implications for the study of human evolution, for example in explaining the craniofacial variation found in the Middle Pleistocene.

8.2.2 Concluding remarks

The data set for this study was collected specifically to address the issue of dispersal around the Indian Ocean rim. One of the main aims of the project that this study was part of was to highlight the practical use of museum skeletal collections to the study of human evolution. It has become evident that in order to fully answer questions regarding the patterns of morphological diversity, a wider geographic range of populations is required. This further demonstrates the necessity of access to skeletal collections in order to continue research in the light of questions raised by current

projects. Lahr (1996) emphasised that analyses based on a greater temporal and geographical scale are essential for the understanding of local populations. To take the conclusions of this study further it would be of interest to collect data from relevant prehistoric material and fossil data that were not included in the original data. Additionally, it would be of particular interest to compare how the morphology of a variety of post-cranial skeletal elements are determined by dispersal events and local adaptations.

Questions of human dispersal are difficult to answer, whether on a global or regional scale. The review of literature on the specific regions as well as the Out of Africa hypothesis (Chapter 1) shows that no consensus can be drawn from the various sources of data. Genetic data, which is seen by some as a fail safe in determining human origins and migrations, can produce many alternate answers. No clear answer, for example, can be given for whether Australia was founded by one or many populations, even including DNA taken from the earliest settlers of the continent (Adcock *et al.*, 2001; Cooper *et al.*, 2001). Genetic data must therefore not be relied on as the only source of information, and data from skeletal morphology should not be discounted. Whilst a greater understanding of the mode and tempo by which craniofacial features evolve is required in order to fully interpret estimates of biological affinity, this study has demonstrated that it is possible to extrapolate migration history from extant human populations. It is clear, however, that when examining for the effects of one specific migratory event all other possible dispersals and subsequent causes of diversity must also be considered. Renfrew (1987) describes the picture that we have of populations today as a palimpsest, whose detail is the product of many processes over the millennia since their foundation. Traces of the Late Pleistocene dispersal along the southern coastal route can be identified within the extant populations today, however the overall pattern of diversity found is created by the many processes discussed in this work.

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