

### 3.3.4.4.3 Ecogeographic studies of the cranial shape

The measurement of the human head of both the living and dead has long been a matter of interest to a variety of professions from artists to physicians and latterly to anthropologists (for a review see Spencer 1997c). The shape of the cranium, in particular, became an important factor in schemes of racial typology from the late 18th Century (Blumenbach 1795; Deniker 1898; Dixon 1923; Haddon 1925; Huxley 1870). Following the formulation of the cranial index by Retzius in 1843 (see also Sjøvold 1997), the classification of humans by skull shape became a positive fashion. Of course such classifications were predicated on the assumption that cranial shape was an immutable racial trait. However, it had long been known that cranial shape could be altered quite substantially during growth, whether due to congenital defect or morbidity or through cultural practices such as cradling and artificial cranial deformation (for reviews see (Dingwall 1931; Lindsell 1995). Thus the use of cranial index of racial identity was suspect.

Another nail in the coffin of the Cranial Index's use as a classificatory trait was presented in Coon (1955), where he suggested that head form was subject to long term climatic selection. In particular he thought that rounder, or more brachycephalic, heads were an adaptation to cold. Although it was plausible that the head, being a major source of heat loss in humans (Porter 1993), could be subject to climatic selection, the situation became somewhat clouded when Beilicki and Welon demonstrated in 1964 that the trend towards brachycephalisation was continuous between the 12th and 20th centuries in East-Central Europe and thus could not have been due to climatic selection (Bielicki & Welon 1964).

Kenneth Beals, however, decided to test of Coon's hypothesis and found a clear concordance between climate and head size and shape (Beals 1972; Beals *et al.*, 1983; Beals *et al.* 1984). Beals' initial paper gathered data on Cephalic Index (CI hereafter) on 339 populations (living), most of mixed sex (Beals 1972: 86). He grouped these samples into zones of climatic stress, representing dry heat (arid), wet heat (tropical), wet cold (temperate) and dry cold (sub-Arctic and Arctic). His results are presented in Table 3.26 and Figure 3.7. Despite a large overlap in ranges, all means are significantly different.

Table 3.26: Descriptive statistics of Cephalic Index for 339 populations of mixed sex divided on the basis of climatic zone, adapted from Beals, 1972: 88.

Variables	N (means)	Min. - Max.	Mean (Weighted)	SD
Dry heat	124	70.2 - 89.0	75.98	3.19
Wet Heat	121	72.9 - 89.5	78.68	3.40
Wet Cold	34	76.9 - 85.5	80.54	2.66
Dry Cold	60	74.6 - 89.4	82.25	3.50

(\* all pairs of means are significantly different at the 2% level or lower (Beals, 1972: 87))

Beals' subsequent papers, written in conjunction with Courtland Smith and Stephen Dodd, explored this research further and attempted to place it in an evolutionary context

(Beals *et al.* 1983, Beals *et al.* 1984). The analysis had mixed results. Using a larger sample ( $n = 362$ ) divided into 82 ethnic groupings and correlated with 11 climatic variables (2 of which were later discarded), Beals' earlier result of a significant relationship with between head size and shape and climate was confirmed, with winter temperature being a more important factor than summer temperature, and temperature being more important than humidity (Beals *et al.* 1983: 433) (see Table 3.26 below). Their most significant finding was that cranial capacity (or cranial volume) was negatively related to temperature, and in particular to temperature of the coldest month. This increase in cranial capacity was also independent of stature indicating that brain size was both absolutely and relatively larger where winters were colder (Beals *et al.* 1984) (Table 3.27).

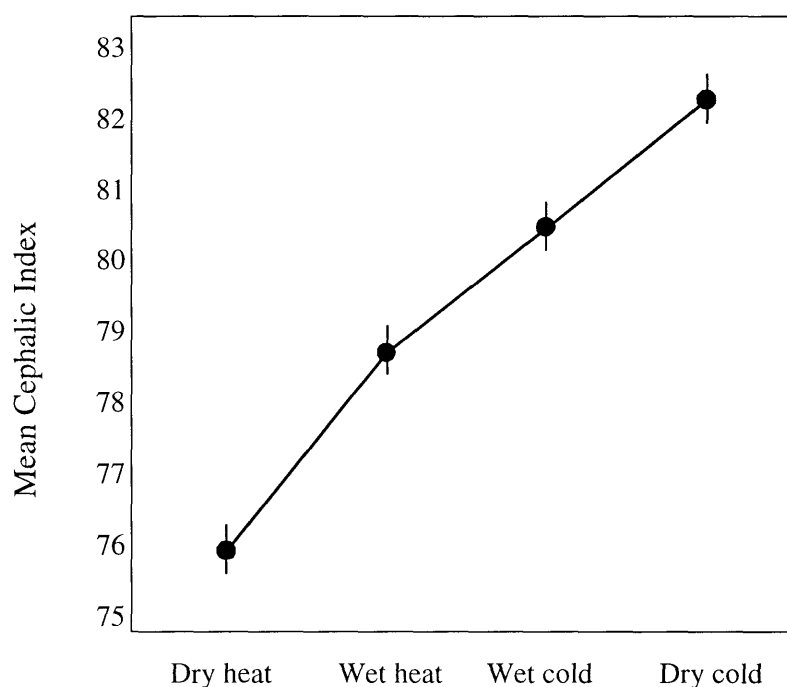


Figure 3.7: Cephalic index vs climate zone, after Beals, 1972: 89.

Table 3.27: Summary of correlations between Cephalic Index and climate variables, adapted from Beals *et al.*, 1983: 431.

Variables	Climatic zone	Winter water vapour	Summer water vapour	Winter temperature	Summer temperature	Annual rainfall
Cephalic Index	0.46***	-0.29**	-0.22*	-0.39***	-0.14	0.03
Cranial Capacity (CC)	0.65***	-0.51***	-0.50***	-0.64***	-0.48***	-0.33**
CC/Stature	0.68***	-0.40***	-0.42***	-0.64***	-0.47***	-0.22*

(\*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ )

In order to test their hypothesis of climatic selection the authors examined Cranial Index (comparable to Cephalic Index as measured on the living) in 111 hominid fossil samples that included specimens of *Homo erectus*, Neandertals and early modern *Homo sapiens*. These samples were divided into climatic zones and it was apparent that for each species (or sub-species) those in colder climates had higher Cranial Indices (Beals, *et al.* 1983: 433). However, the authors also found evidence contra to expectations. They found that CI increased over the period of the Pleistocene in their tropical sample group - a group that should have been the least affected by climate change. There was also a decrease in Cranial Index over the middle to upper Palaeolithic when world temperatures were falling, and then an increase of Cranial Index during the Holocene as world temperatures rose (Beals *et al.* 1983: 435-436). This suggested to the authors that adaptation to climate could not explain all geographic variation in Cranial Index (Beals, *et al.* 1983: 436).

A further study examined the encephalisation issue in human evolution. Using an extended version of their database, they found that not only Cranial Index, but also brain size was related to climate, in particular to winter temperature. Their thesis was that the increase in encephalisation during human evolution could be partially explained by adaptation to cold environments (Beals *et al.* 1984). At the time, this theory was not particularly well received (see comments following (Beals *et al.* 1984: 318-323). However, a later study along these lines was conducted by Freedman, Bulmer and Lofgren (Freedman *et al.* 1991) comparing the endocranial capacity of 73 Aboriginal crania from Western Australia, with a large sample of European crania from Denmark. The authors estimated that up to 66% of the difference in endocranial capacity between the Australian and Danish samples could be ascribed to variation in stature combined with the difference in latitude (Freedman *et al.* 1991: 403), and that these differences might be linked to brain volume via "factors such as surface area and metabolic rate" (Freedman *et al.* 1991: 404).

The role of climate in craniofacial evolution was also examined by Guglielmino-Matessi, Gluckman and Cavalli-Sforza (Guglielmino-Matessi *et al.* 1979) and Albrecht (Albrecht 1980). Both of these studies concluded that adaptation to climate was an important, although not the only, factor in the geographic variation of cranial morphology and that any phylogenetic analysis should take climate into account.

The relationship between head size and shape and climate has also been examined in many of the regional studies already discussed above. Beals' hypothesis of higher CI in cooler climates was confirmed in sub-Saharan Africa by Hiernaux (Hiernaux 1968; Hiernaux & Froment 1976) (see Table 3.28) and in Crognier's studies in Europe and the Mediterranean (Crognier 1981a, 1981b) (see Tables 3.29 - 3.31), although in Africa temperature of the hottest month was found to be a more important factor than the temperature of the coldest month.

Table 3.28: Summary of correlations between cranial measurements of sub-Saharan African males and location and climate variables, adapted from Hiernaux, 1968 and Hiernaux and Froment, 1976: 760-761, Table 1.

Variable	N	Log Rain	Hum+	Hum-	Temp+	Temp-	Alt	Hum range	Temp range
Head L	190	-0.04	0.08	0.04	0.01	0.13	-0.14	-	-
†	213	-0.08	0.00	-0.03	-0.02	0.06	-	-	-
Head B	190	0.24**	0.08	0.28**	-0.33**	0.08	0.10	-0.29**	-0.32**
†	213	0.22**	0.09	0.26**	-0.31**	0.07	-	-	-
Cephalic I	278	0.20	-0.05	0.27**	-0.32**	0.03	0.19**	-	-

(\* significant at 5%; \*\* significant at 1%; † sample sizes and correlation coefficients as in Hiernaux and Froment, 1976: 760-761, Table 1.)

Table 3.29: Summary of correlations between cranial measurements of European, Middle Eastern and North African males and climate variables adapted from Crognier, 1981a: 612.

Variables	n	Mean Ann Temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
Head max length	85	-0.16	0.01	-0.23*	0.07	-0.28	-0.19	0.25*	-0.24*
Head max breadth	85	-0.77**	-0.68**	-0.75**	0.34**	0.55**	0.48**	0.55**	0.32**
Cephalic index	85	-0.54**	-0.57**	-0.48**	0.43**	0.41**	0.50**	0.31**	0.39**

(\*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ )

Table 3.30: Results of Multiple Stepwise regression analysis of cranial measurements of European, Middle Eastern and North African males and climate variables, adapted from Crognier 1981b: 104.

Variables	n	Mean Ann Temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
Head max length	85	9.96	-	-	-	-	19.63	-	2.47
Head max breadth	85	59.25	-	-	-	-	6.78	-	-
Cephalic index	85	-	32.55	-	-	-	17.15	-	-

Table 3.31: Summary of correlations between cranial measurements of European, Middle Eastern and North African females and climate variables adapted from Crognier, 1981a: 613.

Variables	n	Mean ann temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
Head max length	34	-0.13	-0.21	-0.38*	-0.37	0.34	0.02	0.57**	-0.11
Head max breadth	34	-0.62**	-0.49**	-0.64**	0.23	0.30	0.37*	0.46**	0.06
Cephalic index	34	-0.48*	-0.46**	-0.36*	0.41*	0.08	0.02	0.10	0.08

(\*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ )

In Aboriginal Australian populations both Macho and Freedman (1987) and van Holst Pellekaan (1990) found significant relationships between head shape and climate,

although the trends were variable between the sexes (see Tables 3.32 to 3.34). It should be noted that both these studies lack data from populations living in the coldest continuously occupied area of Australia - Tasmania. It is clear from data presented in Birdsell 1993, that both cranial breadth and CI were greatest in Tasmanian Aborigines (Birdsell 1993: 338-344; 383-384) and that this would support Beals' hypothesis. As can be seen in Birdsell's clinal map for this variable (1993: 384, Figure E-35) the distribution of CI over mainland Australia is patchy, although the lowest values do occur in the hot, dry Western Desert region.

Table 3.32: Results of a Stepwise Multiple Regression Analysis on Australian Aboriginal males including cranial measurements and climate variables, adapted from Macho and Freedman, 1987: 44, Table 10.

<b>% Contributions to the regression analysis</b>							
<b>Variables</b>	<b>Rain Jan</b>	<b>Max Temp Jan</b>	<b>Min Temp July</b>	<b>Temp Range Cold Month</b>	<b>Hum Jan</b>	<b>Hum July</b>	<b>Multiple r</b>
<b>Vault</b>							
Head L	-	-	-	-	-	-	-
Head B	4.04**	-	4.75**	-	-	-	0.30**
Head H	-	3.32**	-	6.54**	-	9.14**	0.44**
Head Circ	2.52**	-	20.37**	-	-	-	0.48**
CI	-	-	4.86**	-	-	-	0.22**
H/L I	-	-	-	3.37**	-	-	0.18**
H/B	7.38**	-	-	-	-	-	-

(\* p ≤ 0.05; \*\* p ≤ 0.01)

Table 3.33: Results of a Stepwise Multiple Regression Analysis on Australian Aboriginal females including cranial measurements and climate variables, adapted from Macho and Freedman, 1987: 45, Table 11.

<b>% Contributions to the regression analysis</b>							
<b>Variables</b>	<b>Rain Jan</b>	<b>Max Temp Jan</b>	<b>Min Temp July</b>	<b>Temp Range Cold Month</b>	<b>Hum Jan</b>	<b>Hum July</b>	<b>Multiple r</b>
<b>Vault</b>							
Head L	-	-	-	-	-	-	-
Head B	4.21**	7.60**	-	-	-	4.50**	0.40**
Head H	-	-	-	16.40**	-	-	0.40**
Head Circ	-	-	7.30**	-	-	-	0.27**
CI	-	-	-	-	-	-	-
H/L I	-	-	-	10.49**	-	-	0.32**
H/B	-	-	6.74**	2.45**	-	3.02**	0.35**

(\* p ≤ 0.05; \*\* p ≤ 0.01)

Table 3.34: Summary of correlations between cranial measurements of Australian Aboriginal males and location and climate variables, adapted from van Holst Pellekaan, 1990: 37.

<b>Variables</b>	<b>Latitude</b>	<b>Average Annual Temperature</b>	<b>Min Temp July</b>	<b>Average Annual Rainfall</b>
Bi-Euryon Breadth	0.293*	-0.344**	-0.283*	-
Bi-Asterion	0.329**	-0.349**	-0.364**	-

(Only significant correlations were reported \* p ≤ 0.05; \*\* p ≤ 0.01)

### **3.3.4.5 Experimental Studies: Humans**

#### **3.3.4.5.1 Introduction**

As with other animals, the search for the causes of ecogeographic clines and correlations in humans has been conducted through experimentation. However, the kind of growth experiments in non-human animals, reviewed above, cannot be conducted on human subjects, so the problem has been approached in a different way. The growth of children under different environmental regimes has been studied, but most are observational rather than experimental and the majority test factors of nutrition and/or disease, rather than factors of climate.

Whilst there is a large literature on human physiological adaptation to temperature and humidity, only a subset of these have tested the hypothesis that certain body morphologies are adaptive to heat or cold. These studies tend to be conducted on very small samples of volunteers and test for physiological reactions to either heat or cold stress. The vast majority of these studies have only examined the anthropometric variables of height, weight, surface area and surface area/weight ratio. What is entirely missing (at least to the author's knowledge) are studies that examine the role of body measurements such as bi-iliac breadth and relative limb segment lengths in thermoregulation. Such measurements have also been argued to be under climatic selection and are currently playing an important role in the debate over modern human origins.

#### **3.3.4.5.2 Experimental studies on temperature tolerance with reference to body composition and morphology.**

##### **Heat Stress**

As mentioned above, few studies of the human response to climatic stress examine the relationship between body morphology and acclimatisation. Whilst research has shown that in general all humans can make significant short-term physiological adaptation to the stresses imposed by high temperature and humidity, studies that compare people of different ethnicities also indicate intrinsic differences in adaptation. The source of these differences, however, is a matter of interpretation. As Barnicot (1959) pointed out, it is hard to gauge the relative importance of the factors that might underlie these differences: be they genetic, ontogenetic, or health related.

As an example, both Ladell (1951, 1955) and Wyndham (1966), in comparing the responses of Europeans and Africans to heat and humidity, found that over long term exposure the sweating rate in Africans was below that of Europeans, even when both had reached a similar level of acclimatisation. Wyndham put this down to Africans having an

adaptation to conserve body fluids and/or salts (Wyndham 1966), but Ladell disagreed suggesting it was due to sweat gland fatigue (Ladell 1955). Yet these experiments also revealed that Africans were far less prone to collapse under heat stress than were the control subjects. Similar effects have been found in other tropical populations. Fox found low sweat rates in New Guineans from the Island of Karkar and Lufa in the highlands (Fox *et al.* 1971-72). The authors claim their results indicate that "the New Guinea indigenes are able to maintain thermal equilibrium during their day-to-day living by vasomotor regulation, with relatively little recourse to sweating" (Fox *et al.* 1971-72: 312).

A difference in sweat rates was also found between Europeans and Native Americans. Hanna compared the heat responses of Yaqui and Papago Indians and Mestizos (people of European/Indian ancestry), all life-long residents of the hot, arid region of the U.S.A.'s Southwest, and White American students resident only a short time in Arizona (Hanna 1970). In a test under dry heat conditions the Papago exhibited lower sweat rates and rectal temperatures than the white students. Hanna attributed this to a more effective heat dissipating mechanism in the Papago (Hanna 1970: 191). There were no significant differences between the Yaqui and Mestizos when tested in dry heat, to which they were well adjusted, but both groups were found to be more intolerant to humid heat (Hanna 1970: 187). Those subjects who failed to complete the humid heat test were the heaviest in their respective groups suggesting a disadvantage in having a large body size or a low surface area to weight ratio (SA/W) when exercising in such conditions (Hanna 1970: 193). Hanna's conclusions were that small body size might be adaptive for desert conditions as a smaller body needs less water, and that differences in sweat rates may be due to developmental processes that result in greater densities of sweat glands on the limbs (where sweating is more effective), or a change in the pattern of sweat gland recruitment shifting towards the limbs, so that sweating begins there first (Hanna 1970: 194).

Hanna and Baker (1974) also examined differences in humid heat tolerance between Shipibo Indians and Mestizos from Peru. The subjects walked in the sun for 6 days at 5km/hr and 6 days at 8.5km/hr. The authors found that Shipibo sweated more than the Mestizos over both walking speeds, but at the lower speed showed less cardiovascular stress. Thus the Shipibo were found to be more tolerant to humid heat at lower work rates than were the Mestizos despite similar levels of acclimatisation (Hanna & Baker 1974: 69). However, it should be noted, as Newman has pointed out, that the absolute differences in sweat rates found in these types of studies tend to disappear when they are normalised by weight or surface area (Newman 1975b: 88).

Studies that specifically include body morphology as a covariant in experiments on heat tolerance have produced conflicting results. Robinson found that African American sharecroppers were more tolerant of humid heat than were sharecroppers of European ancestry, and that this was due to the differences in work efficiency and SA/W ratio between the groups (Robinson *et al.* 1941) cited in (Austin & Ghesquiere 1976: 439-440).

Baker also compared African and European Americans. In one of his earliest studies on U.S. servicemen, he concluded that individuals "that have a small amount of body fat, great body linearity and brunette skin can probably march for substantially longer distances in hot deserts than their morphological counterparts" ((Baker 1955) cited in (Baker 1960)). However, in a further study he noted that African Americans were at a disadvantage when exposed to heat in direct sunlight, because their darker skins tended to absorb more heat than did paler skin. Thus he concluded that Africans might be better adapted to hot and humid, than to hot and dry conditions. He also found that African Americans were more tolerant of humid heat than were European Americans, even when groups were matched for body shape and fat percentage (Baker 1959 cited in (Baker 1960: 4). This would seem to suggest that the differences in heat tolerance were due not to body shape, but some other intrinsic factor. However, Baker's overall conclusion was that a large SA/W ratio would be adaptive to hot, humid climates where insolation was low and evaporative cooling inefficient, but not to hot, dry climates where opposite conditions applied (Baker 1960: 7).

In a study of 29 Malaysian-born men aged between 20-33 years and of Malay ( $n = 10$ ), Chinese ( $n = 9$ ), and Indian ( $n = 10$ ) ethnicity, Duncan and Horvath (1988) found that the indigenous Malays exhibited the greatest adaptiveness to a stress test in hot, humid conditions ( $T_{wb} = 32.1$ ). The Malays were the shortest of the test groups and although they had a somewhat lower SA/W ratio than the Indians, they maintained a significantly lower heart rate than the other two groups during the test (Duncan & Horvath 1988: 541). The Chinese sample, whose ancestors were said by the authors to have migrated from "a temperate area" (Duncan & Horvath 1988: 540), were the heaviest group, with the lowest SA/W ratio and performed the least well in the test, having the highest final heart rates, rectal temperatures, oxygen consumption and sweat rate, although the differences for the last three were non-significant (Duncan & Horvath 1988: 541-542). Although the authors argue that the Malay's better performance under the hot, humid conditions may be due to their high SA/W ratio and lower weight for height (Duncan & Horvath 1988: 543), the only significant difference between the Malay and Indian groups is in stature.

Other experimental evidence suggests that a high surface area/weight ratio can be disadvantageous under severe heat stress. When ambient temperature is below critical temperature (between 25°- 27°C (Frisancho 1981: 12), a high SA/W ratio is advantageous particularly where evaporative cooling is possible (for example where humidity is low). However, where temperatures rise above the critical temperature, and where there is very high humidity, or high insolation and/or hot winds, a body with a high SA/W ratio is more susceptible to heat gain than is one with a lower ratio. Several studies have found this effect in smaller, lighter adult men (Austin & Ghesquiere 1976; Strydom 1980), adult women (Bar-Or *et al.* 1969), and male (Wagner *et al.* 1972) and female children (Haymes *et al.* 1974), with those with a higher SA/W ratios performing less well under heat stress than the larger bodied test subjects. On the other hand, there is ample experimental



evidence that large bodied, and/or overweight individuals, performing work "while exposed to a hot environment, are liable to be handicapped by a higher heat strain than their leaner or smaller counterparts" (Bar-Or *et al.* 1969: 408; see also Epstein *et al.* 1983; Miller & Blyth 1958; Schickele 1947; Schwartz *et al.* 1973).

An interesting study conducted by Austin and Lansing (1986) used computer modelling to assess the adaptive advantages of body sizes and shapes at work under different climatic conditions. The body types were denoted "norman" (representing a normal man of about 74.4 kilos), "small man" (lighter than "norman" at 51.25kg, but with "norman" limb proportions), "tallman" (limb segments 10% longer than "norman" with a linear body shape) and short man (limb segments 10% shorter than norman and with a lateral body shape). The first two were used to test Bergmann's rule the last two to test Allen's rule. It was found that in low humidity (30%) and moderate heat (30-35°C) the "norman" and "tallman" types had the thermoregulatory advantage, but that at 40°C the "smallman" had the advantage and "shortman" was at a clear disadvantage with a higher final core temperature and greater heat storage (Austin & Lansing 1986: 158-159). At high humidity (80%) temperature tolerance indicators were inversely related to the SA/W ratio of the body types at 30, 35, 40 and 45°C, however at 50°C the "smallman" type was at a disadvantage because of increased heat load. Because of this Austin and Lansing argue that their pygmoid model (shortman) does not fit in with the theory that Pygmy body size is an adaptation to the hot, humid conditions of the rainforest. This finding, they contended, supported their study on the Batwa and Ntomba (Austin & Ghesquiere 1976). However, it must be noted that conditions of 80% relative humidity and 50°C are unrealistic for rainforest conditions, and further, Pygmies tend not only to be small in body size, but because of allometry have relatively shorter limbs and therefore do not comply with the authors' "smallman" model (Ruff 1993: 54-55). From their simulations the hypothesis that body size and shape are under climatic selection seems to be confirmed, with body shapes conferring high SA/W ratios being advantageous in moderate heat, and the body types with lower SA/W (particularly shortman) having a decreased high temperature tolerance. It also confirms studies that have demonstrated that small body size is disadvantageous where heat stress is severe. The authors conclude that the "model, in fact shows that alterations in body size and shape do affect the outcome of thermoregulatory processes" (Austin & Lansing 1986: 165).

### **Cold Stress**

Current palaeontological evidence suggests that the hominid line evolved in tropical Africa. If so, the movement of hominids into areas of cold climate must have engendered severe adaptive challenges. Thus the study of human adaptation to cold may make a contribution to our understanding of the dispersal and evolution of modern humans. Depending on how the fossil, archaeological, and now genetic evidence is interpreted, these cold adaptations are either extremely ancient, coming from the time after *Homo*

*erectus* ventured north and northeast after about 2mya, or are recent, originating after *Homo sapiens* spread out of Africa about 200-100kya.

As with adaptation to heat stress, there have been numerous studies into the physiological responses to cold. These studies involve either whole body cooling with the subject at rest, or exercise in a cold environment; or the exposure of extremities such as hands or feet to cold. (For a list of studies into hand and foot cooling alone see Steegmann 1975). Most of these studies examine the physical correlates of cold responses, particularly the traits of body weight, fat percentage and SA/W ratio. However, apart from the work of Steegmann (see below), there has been little effort to examine the possibility that other aspects of body morphology may be important in cold adaptation.

The general response of all humans to cold stress is a rise in metabolic rate (producing more heat through exercise or shivering) combined with vasoconstriction in the extremities. In this way the body attempts to retain heat balance by producing and retaining heat in the body core and reducing the loss of heat by radiation and convection from the body shell. In severe cold, vasoconstriction in the extremities is alternated with vasodilation and a counter-current blood flow system that acts to delay cold injury (Frisancho 1981: 43-48).

Despite an overall similarity in the response of humans to cold there are some differences between populations that may be due to genetic selection. For instance, studies comparing Inuit to European controls have found that the Inuit metabolic rate is up to 45% higher. Although their energy rich diet has been implicated in maintaining this high rate, testing has failed to support this as a factor (Frisancho 1981: 62 and references therein). Studies of various other ethnic groups, (eg. Alacaluf (Hammel 1961); Athapasacan (Irving *et al.* 1960); Quecha (Baker 1966b); Japanese Hawaiians (Hanna & Smith 1975); North Asians (Gallow *et al.* 1984); Bushman and Bantu (Wyndham 1966); Saami (Lapps) (Andersen *et al.* 1960)) commonly using Europeans as control subjects, tend to find similar (though smaller than in the Inuit) increases in metabolic rate in response to cold, but acclimatisation may be responsible for at least some of these increases. The stand out exceptions to this general rule are the Australian Aborigines, studies about whom are reviewed below. It has also been found that groups who are exposed throughout their lives to mild to moderate cold, show a much greater tolerance to low temperatures, being able to sleep comfortably at temperatures that European controls find unbearable (Andersen *et al.* 1960; Hammel 1961; Irving *et al.* 1960).

Perhaps the most notable difference in response to cold between groups is that of extremity warming. There appears to be a clear differentiation between tropical Africans and non-Africans. Data from the Korean War demonstrated that soldiers of African ancestry were much more susceptible to frostbite injury than were soldiers of European origin (Steegmann 1967). This was put down to a more effective extremity re-warming response in the Europeans. Studies of populations that are habitually exposed to

conditions that could lead to frostbite injury of the fingers and toes, also show this heightened re-warming response, but to an even greater extent than in the European controls (Frisancho 1981; Little *et al.* 1973, Little *et al.* 1971; Steegmann 1975: 55-76).

Of particular interest to this thesis are studies that link body size and proportions to thermoregulation. Where tested, studies have repeatedly demonstrated that tolerance to cold is linked to the amount of subcutaneous fat and to the surface area to weight ratio of an individual (Baker 1960, 1966b; Baker & Daniels 1956; Gallow, *et al.* 1984; Hanna & Smith 1975; Kollias *et al.* 1974; LeBlanc 1954). These results support the basic contention of Bergmann's rule, however Gallow *et al.* (1984) found that during exercise the advantages conferred by a high fat percentage and a low SA/W ratio were lost.

The proposed thermoregulatory advantages of high fat percentage and low SA/W ratio, along with other body measurements have also been examined by Steegmann in his studies on extremity and facial warming. Steegmann used a sample of 24 European and 33 Japanese males exposed to moving 0°C air for 70 minutes and correlated the whole body and finger temperature responses with 42 anthropometric measurements. There were relatively few significant correlations (see Table 3.35).

Table 3.35: Summary of correlations between mean finger temperature at 40 to 70 minutes exposure to moving 0°C air and other variables, adapted Steegmann, 1974: 627, Table 2.

Variables	<i>r</i> Japanese (n = 32)	<i>r</i> European (n = 20)
Abdominal Skinfold	0.432*	
Pectoral Skinfold	0.362*	
Relative Sitting Height	0.408*	0.436*
Cephalic Module	0.372*	
Head Size Index (Cephalic index + Face Breadth + Face Height)	0.367*	

(\* p < 0.05)

These results show that in the Japanese group individuals with larger abdominal and pectoral skinfolds (that is more body fat on the ventral trunk), relatively longer trunks, and larger heads, maintained higher finger temperatures. In the smaller European sample the only significant correlation was with relative sitting height. The positive correlation between finger temperature and greater relative trunk length, is seen by Steegmann as "a major result of this research" (Steegmann 1974: 637), however his results are not particularly strong. The anthropometric measurements that did not correlate with skin temperature included weight; stature; chest circumference; head length, breadth, and height; horizontal and vertical head circumferences; face breadth, height and protrusion; nose breadth and height; skinfolds of the scapular, triceps, knee, malar and cheek; head and total surface area; SA/W ratio; total skinfolds; estimated percent body fat; cranial index; facial index; nasal index and skin reflectance measurements (Steegmann 1974: 622). This list is interesting as it contains many aspects of body morphology often touted as

being important in thermoregulation or, at least, under climatic selection. Steegmann himself was somewhat equivocal about his results due to the modest correlations and suggested that:

"correlations improved in strength during the second part of the exposure period would be predicted since morphological adaptation is clearly more ponderous than physiological, strengthening the interpretation that temperature is more dependant biologically on morphology only where other resources begin to fail (Steegmann 1974: 630).

In another part of this study Steegmann correlated facial skin temperatures with anthropometric measurements. As in the finger warming experiment he found sitting height to be an important factor with a larger absolute sitting height related to higher forehead temperature in his Japanese sample, and a larger relative sitting height to raised chin temperatures in his European sample (Steegmann 1972: 200-215). However, contra to expectation, he found that increased linearity (measured by Lefrou's Index) was associated with increased cheek temperature in the Japanese males (Steegmann 1972: 200-215). Overall, however, there was little covariance found between gross body measurements and skin temperatures.

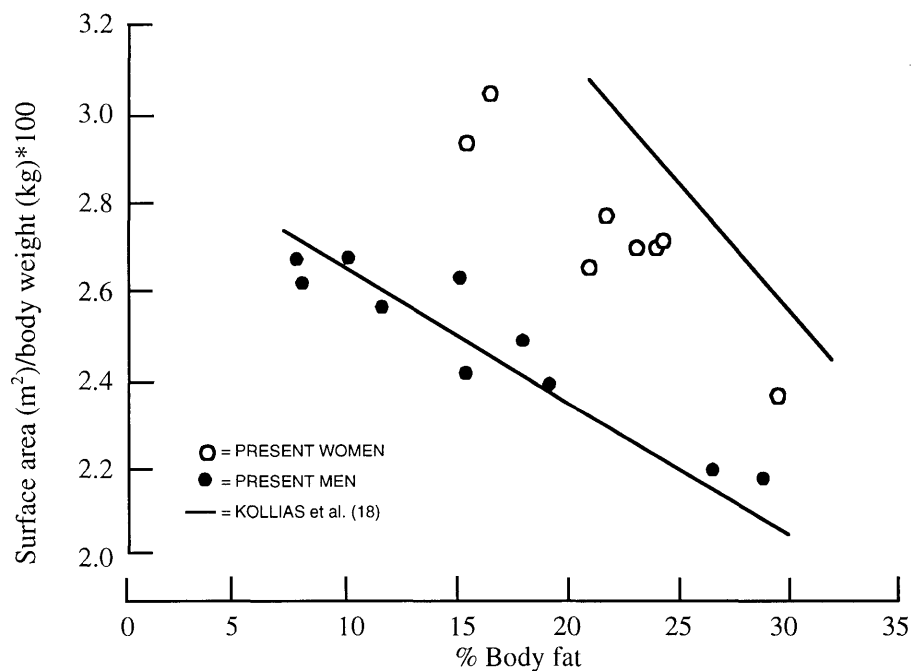


Figure 3.8: Per cent body fat vs SA/W ratio in males and female, after McArdle *et al.* 1984: 1570.

The problem of the differential advantages of fat or SA/W ratio in thermoregulation has been explored in studies that compare males and females. McArdle and his co-authors found that SA/W ratio to be the main factor in the retardation of heat loss

(McArdle *et al.* 1984). The authors compared 8 females and 10 males in successive 1-hour immersion tests at 20, 24 and 28°C. They concluded that "... under identical conditions of cold exposure and body fatness at rest, women would tend to cool at a faster rate than men, through a smaller and less active mass across a relatively larger surface area" (McArdle *et al.* 1984: 1571). As can be seen in Figure 3.8, for any percentage of body fat a woman has a much higher SA/W ratio than a man. Because of their higher SA/W ratio the extra body fat that women tend to carry confers no thermal advantage.

### **Experimental studies on temperature adaptation in Australian Aborigines**

To end this section, studies that have examined the ability of Australian Aborigines to adapt to thermal extremes will be reviewed, as it is important to gauge the extent to which physiological adaptations may have occurred and whether they may be of more importance than morphological adaptations.

Although it was clear that Aboriginal people were well adapted to hot conditions, physiological research was instigated by the observation that Aboriginal people living in arid regions could sleep comfortably with very little shelter in cold conditions. In inland Australia night time temperatures can regularly fall to near or even below freezing (Bureau of Meteorology 1975). Sir Stanton Hicks was the first researcher to systematically test these observations. His Aboriginal subjects were found to have a unique physiological response, in that their resting metabolism during sleep did not rise with exposure to cold (Hicks & Matters 1933; Hicks *et al.* 1931; Hicks *et al.* 1934) whilst their deep body and skin temperature fell quite dramatically (Goldby *et al.* 1938; Hicks & O'Connor 1938a, 1938b). The Aboriginal subjects could sleep comfortably with skin temperatures of about 27-28°C, and with the temperature of the feet even lower. At rest, mean human skin temperature is usually about 30°C (Clark & Edholm 1985: 67). In such conditions Europeans find it extremely difficult to sleep and tend to compensate by raising the metabolic rate and thus skin temperature (see above). These results were confirmed in later research (Hammel *et al.* 1959; Scholander *et al.* 1958). This adaptation was found to involve the restriction of blood supply to the skin thereby increasing effective insulation. It has been argued that "the ability to permit the body temperature to fall in this fashion reduces heat loss from the body and the absence of shivering permits sleep and conserves energy requirements" (Macpherson 1966: 438). This may represent a method of saving energy where food resources are not adequate enough to supply the extra energy needed to raise the metabolism during cold exposure, as occurs in many other ethnic groups (Kirk 1981: 157-158). The response to cold of Aborigines living in the tropics was also investigated and whilst they were found to be more sensitive to cold and did raise their metabolism, the response was not as great as in the European controls (Hammel *et al.* 1959).

Studies of the response of Aboriginal individuals to heat have also been conducted. Wyndham and his associates found that when compared to Europeans, their Aboriginal

subjects (from the tropical north) maintained similar heart rates and body temperature, but sweated much less (Wyndham et al. 1964), a result similar to that found in tropical Africans and some Native Americans. This physiological adjustment is usually seen as an adaptation to conserve moisture and electrolytes (Macpherson 1966: 440).

### **3.3.4.5.3 Experimental studies on temperature tolerance with reference to the morphology of the head and face**

Over several papers Steegmann examined the hypothesis of Coon, Garn and Birdsell (1950) that the typical facial features of Asian or Mongoloid peoples (wide-flat faces, non-protruding noses, fat-padded cheeks) were the result of adaptive selection to severe cold. The results of his experimental research were to entirely discount the cold-engineered face theory. His experiment on the effect of cold on cranio-facial growth in rats and his review of the literature on cold injury, have been reviewed in previous sections.

In an initial experiment on human subjects, he exposed 11 Japanese-American males and 15 European-American males to 90 minutes of cold at 1°C (Steegmann 1965: 355-356). Although the Japanese males were able to maintain higher facial skin temperatures than the European samples, correlations between skin temperatures and facial form were not significant (Steegmann 1965: 359). Steegmann found that the higher skin temperatures were apparently due to a more active hunting response (cyclic re-warming of skin surface) in the Japanese subjects (Steegmann 1965: 359-360). Steegmann argued that this difference was genetic in nature (Steegmann 1965: 361). In a later experiment he exposed a sample of 33 Japanese Hawaiians and 25 European Hawaiians to 70 minutes of cold at 0°C. His results were somewhat different, with only the temperature of the forehead being higher in the Japanese sample at the end of the experiment, and the Europeans showing a higher frequency of hunting response (Steegmann 1972: 213). The results of the correlation study are summarised in Table 3.36.

As the results show, the Japanese facial- skin temperatures correlated with more cranio-facial variables than did the European sample and the samples shared few correlations in common. Whether this is due to chance because of small and unequal samples sizes or is a reflection of biological differences between the groups is uncertain. However, the overall results demonstrated that, contra to Coon's hypothesis, larger and more protrusive malars were associated with lower skin temperature on the cheekbones, and that the temperature of the nose was unrelated to nose shape or protrusion, but instead varied positively with head size. As for the proposed thermal advantage of fat padding, it was found that increased sub-cutaneous fat decreased facial skin temperatures, thus was no protection against frostbite. These results certainly put the "cold-engineered Mongoloid face" theory to rest, however they seemed to fit the "Neandertal cold-engineered face theory", also originally put forward by Coon, almost perfectly (Steegmann 1972: 218).

Table 3.36: Summary of correlations between facial skin temperature after 70 minutes of exposure to moving 0°C air and other cranio-facial measurements, adapted from Steegmann, 1972: 200-212.

Skin temperature at:	Cranio-facial variable	<i>r</i> Japanese (n = 33)	<i>r</i> European (n = 25)	
Forehead	Malar skinfold	0.441*	-	
	Head length	0.349*	-	
	Face length	-	0.400*	
Malar	Sagittal face protrusion	0.486**	-	
	Relative sagittal face protrusion	0.473**	-	
	Alae-Malar angle no.5	0.437*	-	
	Bizygomatic width	-0.424*	-	
	Sagittal nose angle no.2	-0.418*	-	
	Combined transverse face protrusion I	0.412*	-	
	Facial Index	0.405*	-	
	Relative transverse face protrusion	0.403*	-	
	Malar index no.1	-0.371*	-	
	Malar index no.2	0.370*	-	
	Cheek skinfold	-0.344*	-	
	Cephalic module	-	0.453*	
	Head height	-	0.453*	
	Head:total SA ratio	-	0.403*	
Cheek	Cheek skinfold	-0.482**	-	
	Cheek thickness	-0.449**	-0.583*	
	Malar index no.2	0.425*	-	
	Transverse chin radius	-0.410*	-	
	Relative sagittal nose protrusion	-0.352*	-	
	Face module no.2	-0.352*	-	
	Malar arc Q	-0.342*	-	
	Head:total SA ratio	-	0.443*	
	Chin	Sagittal chin angle	0.367	-
		Nose	Cephalic module	0.435*
Head surface area	0.358*		-	
Head length	0.352*		-	
Head:total SA ratio	-		0.553*	
Alae-Malar angle no.5	-		0.470*	
Malar index no.2	-		0.434*	
Cephalic index	-		-0.400*	

(\*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ . Descriptions of indices and angles can be found in Steegmann (1972))

### 3.3.5 Are Bergmann's and Allen's Rules Thermoregulatory in Nature?

There are two major lines of objection to the significance of the ecogeographic rules of Bergmann and Allen. The first emphasises exceptions to the rules and notes the importance of physiological and behavioural adaptations: at its extreme this can lead to a complete rejection of the existence of these rules. The second accepts that clines in body size and shape exist but deny they are linked to thermoregulation.

There are a number of researchers who have argued that the ecogeographic rules have no adaptive significance (Geist 1987, 1990; Irving 1957; McNab 1971; Rosenzweig 1968; Scholander 1955; Van Voorhies 1996, 1997; Wilber 1957) (see also Table 3.37). Interestingly much of the heat in the debate has been over whether ecogeographic rules apply to humans.

Scholander was one of the most vehement critics of Bergmann's and Allen's rules. He felt that physiological and behavioural adaptations were of more importance than

changes in size and shape (Scholander 1955: 17-19). In challenging the presumed physiological basis of Bergmann's rule, he argued that:

“From a purely physiological standpoint, if relative surface reduction were a point of general adaptive importance, we should expect this to modify the animals not only on a subspecific level, but the whole northern warm-blooded fauna should by convergence tend towards large globular species. This is quite obviously not so. ... We may conclude that there is no physiological evidence to indicate that those cases of subspecific clines which accord with Bergmann's and Allen's rules are the result of a heat-conserving adaptation” (Scholander 1955: 22-23).

Irving came out in support of Scholander's views pointing out that the:

“difficulties encountered in postulating adaptive value for the inflexible surface-mass relations contributed importantly to development of the idea that flexible insulation best described conditions of thermal exchange between the homoiothermous animal and its surroundings” (Irving 1957): 258).

Wilber, meanwhile, disputed the assumption that there was a simple relationship between heat production and body size, and heat dissipation and surface area (Wilber 1957: 330). Like Scholander he noted that animals had evolved various biological and behavioural mechanisms to retain or dissipate heat. He maintained that the ecogeographic rules were of "historical or descriptive interest only" and were not valid generalisation relating the adaptations of animals to cold (Wilber 1957: 332). He suggested that it was the readjustment of cellular mechanisms and not changes to body morphology that was the important factor in heat regulation (Wilber 1957: 332). The importance of insulative and physiological adaptation to temperature was emphasised in the comprehensive review by Hart on thermoregulation in homeotherms published around the same time (Hart 1957).

Mayr (1956; 1963), however, dismissed these arguments claiming that they were based on "semantic misunderstandings and insufficient analysis" (Mayr 1963): 310). In particular, he notes that many of the objectors fail to understand that the rules are a population phenomenon and that the "validity of these empirical findings is independent of the physiological interpretation given to the observed regulations" (Mayr 1963: 319). Still, a search of the recent literature can come up with exceptions to the rules (see Table 3.37) and certainly Mayr agrees that there are exceptions, such as those found in burrowing animals or migratory birds. The vast majority of evidence, however, does confirm that these intra-specific "regularities" in body size and shape exist in a wide range of taxa.



Table 3.37: Empirical studies questioning the existence and/or adaptive significance of ecogeographic rules in non-human animals.

Reference	Taxon	Comments
Ray 1960 (Rosenzweig 1968)	Ectotherms Mammalian carnivores	Found Bergmann and Allen-like size clines in a wide range of ectotherms but questioned the thermoregulatory explanation. Body size correlated more highly with primary plant production than with temperature or latitude.
(McNab 1971)	Mammalian carnivores	Body size of carnivores in Nth America were found to be due size of prey and species competition. However, this finding was criticised by Grant (Grant 1972).
(Johnston and Selander 1973)	House Sparrow	Body size variation in European House Sparrow is contra to Bergmann's rule.
(Kolb 1978)	Fox	Body size in foxes correlated with winter night-length (hours available for hunting), resulting in a south to north increase in body size.
(Wasserman and Nash 1979)	Deer Mouse	Body size of deer mice, <i>Peromyscus maniculatis</i> , didn't change with altitude, but hair length did.
(Murphy 1985)	House Sparrows	Body size clines in House Sparrows are linked to seasonal availability in food resources. Larger bodied birds are better able to resist winter starvation.
(Geist 1987, Geist 1990)	Endotherms	Geist argues that body size clines in cold-blooded species are due to the length of the growing season and the correlations with temperature are spurious.
(Godfrey et al. 1990)	Lemurs	Largest sub-fossil lemurs were found in wetter areas indicating that body size was related to "richness of the plant community" not to temperature.
(Mugaas and Seidensticker 1993)	Racoon	Although the body mass of the Racoon appears to follow Bergmann's rule the authors argue that a racoon with a larger body is better able to resist starvation during winter and the size cline is not related to thermoregulation but to seasonal food availability.
(Remsen 1993)	<i>Atlapetes rufinucha</i>	Geographic variation in size of <i>Atlapetes rufinucha</i> in the southern Andes does not support Bergmann's Rule.
(Yom-Tov 1993b)	Striped mouse	Body size clines in the striped mouse of South Africa did not follow Bergmann's rule.
(Brumfield and Remsen 1996)	Cinnycerthia Wrens	Size variation within populations was found to be inconsistent with Bergmann's Rule, and cross species variation being counter to it with the smallest species occurring farthest from the Equator.
(Sullivan and Best 1997)	Kangaroo rat	Large kangaroo rats were found to inhabit warm and arid southernmost latitudes, whereas smaller animals were found in relatively cool and moist regions to the north. Thus body size is linked to temporal variation in availability of food.
(Van Voorhies 1996, Van Voorhies 1997)	Ectotherms	Argues that Bergmann-like size clines in ectotherms are due to developmental processes on the cellular level and have no adaptive significance.

But doubters remained (and still do). In 1968 Rosenzweig examined body size clines in mammalian carnivores (Mustelids, Vulpids and Canids) in relation to ecosystem productivity, temperature, latitude, competitive pressure and prey size. He found that both temperature and latitude were equally good predictors of body size. Because of this he argued that temperature could not be the direct cause of the size clines and that total primary production, as measured by actual annual evapotranspiration (AE), was a better correlate, with competitive pressure and prey size being only secondary predictors. This is because a "carnivore's body size depends not only on its prey size, but also on the rate at which it can obtain energy" (Rosenzweig 1968: 310). Although AE was found to be a good predictor this only held true "in environments poor in water or heat or both. I interpret this to mean that if food is in short supply, as in deserts or tundra, body size will be limited by food supply. If AE is very high in an environment, however body size and AE are not correlated or else are negatively correlated" (Rosenzweig 1968: 309).

Another study to examine size clines in mammals and especially carnivores was that of McNab (1971), although he was to disagree with Rosenzweig's conclusions. McNab argued that the main flaw of studies that considered a small SA/W ratio as being a selective advantage in the cold was that they suggested "that there is a reduction in the absolute amount of heat loss through a surface by a relative reduction in surface area" (McNab 1971: 845). This, however, he contended, was impossible as large "individuals of a species lose more heat via their surface than small individuals ... because large individuals have larger surface areas than small individuals" (McNab 1971: 846). He examined a variety of mammal species both carnivores and non-carnivores, and concluded that in carnivores, body size was primarily scaled to prey size (McNab 1971: 851-852).

In a more recent challenge to the thermoregulatory orthodoxy, Geist (1987, 1990) strongly criticised the view that Bergmann's rule is a "concept of acknowledged validity" (Geist 1987: 1035) and suggested that body size correlates not with temperature, but with the length of the growing season, and that this is proven by the reversal of body size clines in the high latitudes above 60° N. He also agreed with Scholander's view that changes to body insulation are a more effective adaptation than are changes in body morphology (Geist 1987: 1037). Despite his vehemence it is quite clear from his own diagrams (1987: Fig 1 and 2: 1036) that body size is positively related to latitude between 0° and 60°N, a situation noted by Paterson in his critique of Geist's paper (Paterson 1990: 1610).

Another major disagreement lies in the apparent latitude-related body size clines in ectotherms (Ray, 1960; Lindsey 1966). As ectotherms cannot produce their own body heat it would seem impossible that thermoregulation was responsible for these clines (McNab 1971). Indeed Ray stated that "Bergmann's and Allen's Rules say nothing about heat conservation. ... That the onus of heat conservation has become attached to them is

unfortunate." (Ray 1960: 105). Van Voorhies (1996; 1997), observing nematodes and fish, has suggested that the size clines were the result of an increase in cell size of ectotherms growing at colder temperatures. Thus the clines are due to phenotypic plasticity. His hypothesis has been challenged by Mousseau (1997) and Partridge and Coyne (1997). Mousseau argues that growing-season length is responsible for size clines in insects; in fact he notes that body size clines in many insects follow the converse of Bergmann's rule (Mousseau 1997: 630-631). Partridge and Coyne, on the other hand, provide evidence to support temperature as being responsible for the body size clines, with fruit flies raised over many generations at lower temperatures evolving larger size (Partridge & Coyne 1997: 633). Further they argue that the phenotypic plasticity itself is likely to be under natural selection (Partridge and Coyne 1997: 633).

The notion that size clines are due to developmental plasticity has also been mooted for humans. Some researchers have implicated temperature as a factor in influencing human development (Eveleth 1966; Hanna *et al.* 1989; Little & Hochner 1973; Mills 1942: 145). For others, nutrition is often seen as an important, if not key factor, in determining adult body size and is argued by some to be the basis of the body size clines observed in ecogeographic studies (Endo *et al.* 1993; Hiernaux 1968, 1974; Newman 1953, 1956, 1960, 1975a; Newman & Munro 1955; Walter 1976). This is supported by numerous studies on human growth (Eveleth & Tanner 1976; Tanner 1966) and secular changes in populations exposed to better nutrition and health care (Boas 1912; Fishberg 1905; Froehlich 1970; Goldstein 1943; Ito 1942; Lasker 1946, 1952; Lasker & Evans 1961; Shapiro 1931, 1939; Tanner *et al.* 1982; Van Wieringen 1986). However, although nutrition must be responsible for some of the variation, it is clear that body size, particularly stature, is highly heritable (Susanne 1977: 576) and thus determined largely through genetic control. This has been demonstrated in the various Pygmy or pygmoid groups, where small body size has been achieved through several different genetic mechanisms affecting growth hormone pathways (Shea 1992: 125-126). No amount of extra food will ever make the average Pygmy stand as tall as the average Dinka.

Another interesting alternative has been posed by Vrba (1994; 1996). She suggests that temperature can directly affect growth via the endocrine system. Citing evidence of a direct association of hormone production (from the hypothalamus, pituitary and thyroid), growth duration, growth rate and temperature in salamanders and rats, she contends that exposure to cold temperature changes the levels of hormone production leading to a larger body size (hypermorphosis) with relatively reduced extremities (paedomorphosis) (Vrba 1994: 355).

The results of some distributional and temperature tolerance studies have also produced results interpreted as contradicting Bergmann's and Allen's rules. The proposed thermal advantages of a high fat percentage and low SA/W ratio in cold conditions has been challenged. In a study of 10 indigenous groups Elsner found no

correspondence between levels of body fat and climate suggesting that without adequate nutrition high levels of body fat cannot be maintained (Elsner 1963). Wyndham (1966) also strongly challenged the assumptions behind Bergmann's and Allen's rules, arguing that the results of his temperature stress tests on Africans and Europeans demonstrated no thermoregulatory advantages of differences in SA/W ratio. Budd *et al.* (1991), in examining the effects of age, fitness and fatness on male whole-body responses to cold, found that age had a negative effect due to a progressive decline in vasoconstrictor response, but an increase in fatness could ameliorate this effect. This aging effect starts quite early in life, beginning in the mid-twenties (Budd *et al.* 1991: 2387). This may suggest that SA/W ratio is of less importance than either vasomotor control or fat percentage in thermoregulation. In terms of heat adaptation, Newman has noted that there appears to be only one human response to heat stress (Newman 1975b: 90) and points out all the available studies "reveal very few differences that are not presumably a function of the states of heat acclimatization and physical fitness in each group at the time of study" (Newman 1975b: 87-88).

### 3.3.6 The Ecogeographic Rules and Human Evolution

Logic would suggest that if the bodies of modern humans are subject to developmental plasticity and/or long-term genetic selection in response to climate, then these same forces must have acted in similar ways upon our hominid ancestors. Some researchers have argued that the cyclic climatic changes of the Pleistocene were ultimately responsible for the emergence of the hominid line, while others have concentrated on those hominids that moved out of the tropics and into temperate regions, where they faced new and often severe cultural and biological challenges.

Such a scenario was first suggested in 1927 by Hrdlicka (cited in (Trinkaus and Shipman 1992: 236) to explain Neandertal morphology, particularly the classic or western European Neandertals who are known to have lived in the glacial cold of the last (or Würm) glaciation. Some years later this theme was to be revisited. The western Neandertals are distinguished by robust postcrania and a wide pelvis, a barrel-shaped chest (as evidenced by long "S"-shaped clavicles and strongly curved ribs), indicating a broad stocky body with a high weight for height. They also had shorter limbs relative to height, particularly short distal limb segments, and a large cranium and face, a projecting mid-face and a very large and projecting nose. A number of authors have linked these features with cold adaptation. The broad, round trunk, large weight for height and foreshortened limbs are suggestive of both Bergmann's and Allen's rules (Coon 1962, 1982; Holliday 1997a, 1997b, 1999a; Ruff 1991, 1993, 1994; Trinkaus 1981; Trinkaus and Shipman 1992). The facial and nasal development is argued to help insulate the brain from cold and to assist in warming and/or moistening inspired air, or alternatively, regaining moisture from expired air (Coon 1962: 534; Brose and Wolpoff 1971: 1178; Franciscus 1989; Wolpoff 1995: 677; 681-682).

Trinkaus (1981) was the first to systematically examine the hypothesis that Neandertal body shape was cold-adapted. His stated aim was to "analyse these extinct hominids in terms of the adaptive significances of their morphological patterns rather than in terms of a strictly phylogenetic framework" (Trinkaus 1981: 187). Looking specifically at limb proportions he compared 13 suitable European and Levantine Neandertal individuals, to a range of anatomically modern humans from the Near East and Europe dating from the Late Mousterian, through to the Upper Palaeolithic to the recent period. Whilst Trinkaus found that the ratio of upper to lower limb lengths were statistically identical between Neandertals and modern humans (Trinkaus 1981: 189), it was clear from his analysis that the crural (tibio-femoral) and brachial (radio-humeral) indices demonstrated a distal shortening in Neandertal limbs, which were only approached by modern human populations such as the Saami, Inuit and modern Europeans who live in cold climates (Trinkaus 1981: 193- 208). To support the contention that cold adaptation was involved he used regression analysis on a number of recent human osteological samples. Trinkaus found a coefficient of  $r = 0.86$  ( $n = 12$ ,  $p = 0.004$ : my calculation) between brachial index and mean annual temperature and  $r = 0.81$  ( $n = 14$ ,  $p = 0.004$ ) between crural index and temperature in these groups. Of most interest, though, was the absence of distal limb shortening in the European Upper Palaeolithic sample. These groups not only had absolutely longer limbs but also had higher brachial and crural indices. If short distal limb segments were a cold adaptation the question is why did these humans, living through the last and most severe glacial episode, not display limb shortening? Trinkaus' answer was that they were recent migrants to Europe from warmer areas (Trinkaus 1981: 216). This evidence has been used to support a hypothesis of replacement of the Neandertals by modern humans coming from the warmer south or southeast (Stringer & Andrews 1988; Stringer 1992). Trinkaus did not find conclusive evidence to suggest an *in situ* evolution of the Upper Palaeolithic and later populations towards cold adapted body proportions (Trinkaus 1981: 216-217), however two other researchers have examined this issue further.

The first was Jacobs, who in two papers examined the body proportions of Upper Palaeolithic and Mesolithic populations (Jacobs 1985a, 1985b). The first paper examined variation in long bone morphology and body proportions. His samples were divided into Pre-Glacial Maximum, Late Glacial and Post-Glacial; the former two representing the Upper Palaeolithic and the latter the Mesolithic. Between these two time periods he found "a sizeable reduction in long bone lengths" (Jacobs 1985a: 311) with the greatest reduction being between the Pre-Glacial and Late Glacial groups. There were differential patterns of response between males and females, with the females continuing to become smaller over all time periods (Jacobs 1985a: 313). Measures of robusticity were inconclusive, however there appears to be an increase in robusticity, as evidenced by articular size, between the glacial and post-glacial periods (Jacobs 1985a: 315). This may indicate that while the later groups were smaller, they were also relatively heavier for

their height. As for body proportions the situation is less clear cut. If the Pre-Glacial and Late Glacial groups are combined there is a clear reduction in distal limb segments over time. But as can be seen in Table 7 of Jacobs' paper, if the groups are considered separately then it appears that compared to the Pre-Glacial groups, the Late Glacial group does not have the reduced limb segment proportions expected if cold adaptation had occurred (Jacobs 1985a: 319).

This paradox was explored in Jacobs' second paper. He first demonstrated cold adaptation for his Mesolithic sample by calculating the correlation coefficients between the average winter temperature of the samples' location and the claviculo-radial, brachial and crural indices. His results are reproduced in Table 3.38.

Table 3.38: Correlations of limb indices of Mesolithic human fossils with winter temperature, adapted from Jacobs, 1985b.

Index	Males		Females		Pooled Sexes	
	n	r	n	r	n	r
Claviculo-radial	14	-0.38	9	-0.63*	23	-0.45*
Brachial	19	0.30	11	0.50*	30	0.36*
Crural	18	0.38*	13	0.18	31	0.30*

(\*P<0.05)

In both males and females the correlations reveal a pattern of distal limb segment shortening in colder regions, however the patterns are different between males and females. In the male sample, despite its having a larger sample size, the only significant correlation is between crural index and temperature, whereas the females exhibit relatively large and significant correlations between claviculo-radial and brachial indices and temperature, but not between crural index and temperature. Jacobs suggests that this is due to the well-known fact that males are "more developmentally susceptible to short-term environmental factors" whereas the developmentally hardier morphology of females "should more closely correlate with longer-term invariant aspects of habitat" such as climate (Jacobs 1985b: 513). Although the Mesolithic sample suggested cold adaptation, as mentioned above, for the Upper Palaeolithic sample he found contrary results. Despite having apparently lived through some of the worst cold of the last glacial, their limb proportions were less "cold-adapted" than the Neandertals and intermediate between his Mesolithic samples. Jacobs concluded from this that Upper Palaeolithic groups were periodically "displaced southward during the more severe climatic phases of the late Würm, to re-expand northward during subsequent ameliorations" thus explaining their intermediate cold-adaptation (Jacobs 1985b: 513).

Holliday has also examined the issue of cold adaptation in Neandertals and anatomically modern human populations using bivariate and multivariate statistical procedures (Holliday 1997a, 1997b, 1999a; Holliday & Falsetti 1995). In his paper on Neandertal body proportions he compared his Neandertal individuals (n = 6) with a

comparative sample of recent human groups ( $n = 15$ ) (Holliday 1997a: 247). As predicted by Allen's rule he found significant negative correlations between latitude and the brachial ( $r = -0.75$ ) and crural ( $r = -0.88$ ) indices, and a positive relationship with relative femoral head size ( $r = 0.69$ ) (Holliday 1997a: 249). In both his bivariate and multivariate analyses (PCA on logged absolute and Mosimann-type shape variables (Mosimann and James 1979)) he found that in multivariate space the Neandertals were closest in shape to those populations currently residing in cold climates such as the Inuit and northern Europeans (Holliday 1997a: 249-253). In his bivariate plots of his PC scores there was considerable overlap between groups, however by extracting principle coordinate scores and fitting a minimum spanning tree (Figure 3.9), it is clear that, while the Neandertals are morphologically distinct from all recent human groups, they are closest to the Inuit, next closest to the Europeans and furthest from the tropical Africans (Holliday 1997a: 253-254). His analysis indicated that the Neandertals had evolved a "hyperpolar" morphology through selection and that this may have been the result of a lower degree of cultural buffering as compared with the Upper Palaeolithic and later human groups (Holliday 1997a: 255).

Using similar methodology Holliday has examined body proportions in Upper Palaeolithic and Mesolithic groups in the context of the competing hypotheses explaining the appearance of modern humans in Europe (Holliday 1997b). The EUP sample was found to cluster with the recent Sub-Saharan African groups and was distinct from both the other fossil and recent Europeans groups (Holliday 1997b: 440) (see Figure 3.10). In contrast the LUP and Mesolithic samples were more akin to recent Europeans and distinct from Sub-Saharan Africans. This pattern is seen as due to gene flow, with or without total replacement of the Neandertals, followed by the adaptation of these groups to a cold climate (Holliday 1997b: 444). The hypothesis of gene flow from Africa was strengthened with Holliday's confirmation that the early modern humans of West Asia (Skhul-Qafzeh) also had linear (or heat adapted) body proportions (Holliday 1999b).

In a recent paper Holliday has explored this issue further by examining the intrinsic variability of limb and limb segment lengths (Holliday 1999a). Utilising univariate (CV,  $t$ -test and ANOVA) and bivariate statistical methods on his sample groups, Holliday found that unlike in recent humans, the crural and brachial indices of his fossil sample were not correlated with total limb length. In recent humans there is a general morphological pattern that sees increases in brachial and crural indices and absolute limb lengths and/or a decrease in trunk length in warmer climates. This pattern was absent in his EUP, LUP and Mesolithic samples. Holliday discovered that the EUP sample had long limbs and high indices, yet the LUP and Mesolithic groups showed a reduction in limb length, but a retention of high indices (Holliday 1999a: 560). Holliday explained away this paradox as indicating a slow, mosaic evolution in these European groups in response to cold climate, with stature being less adaptively conservative than body proportions (Holliday 1999a: 561-563).

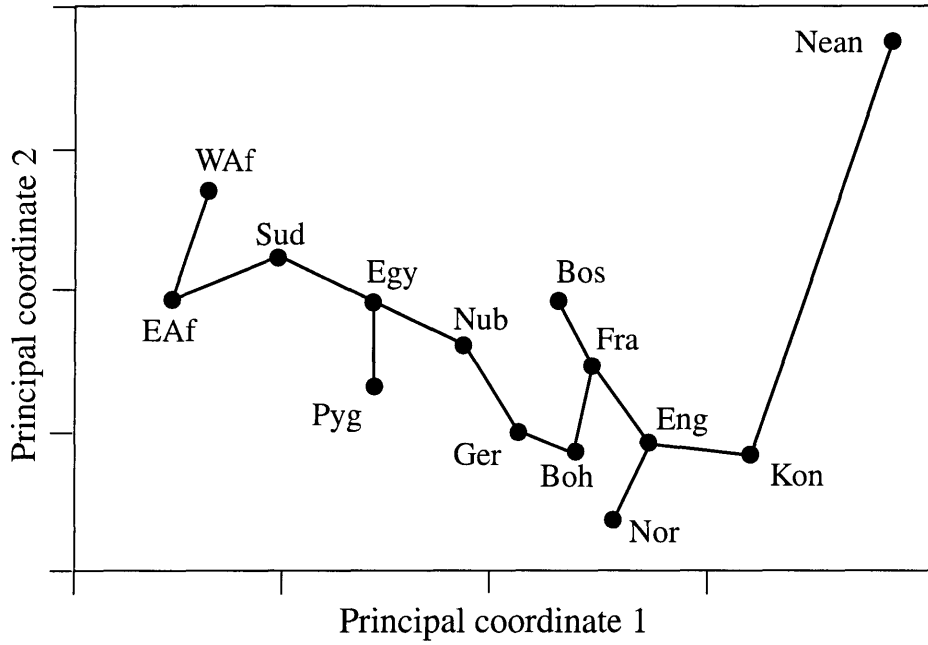


Figure 3.9: Minimum spanning tree, after Holliday 1997a: 254

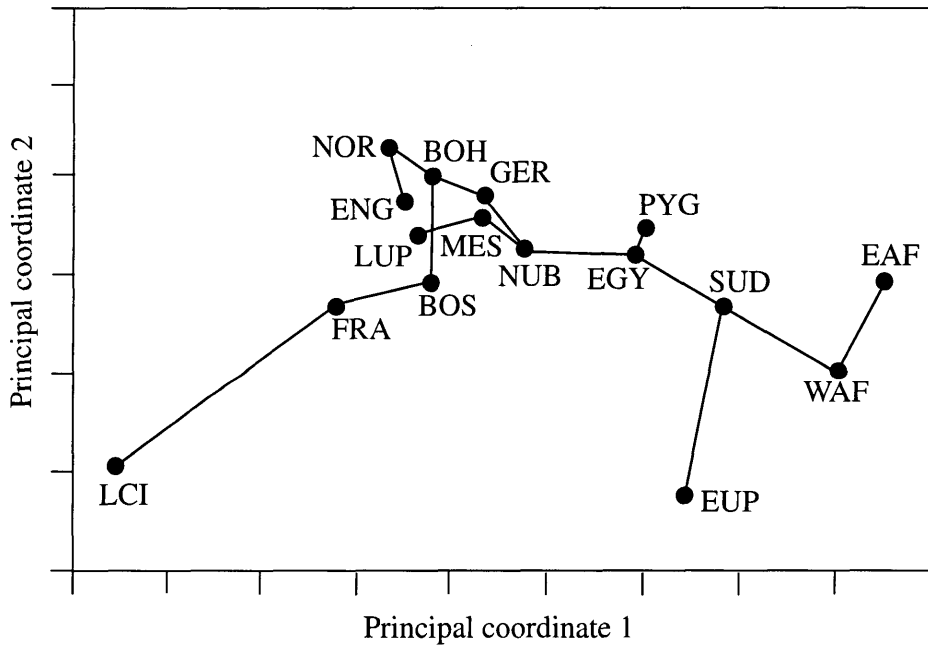


Figure 3.10: Minimum spanning tree, after Holliday 1997b: 440.



All of the studies reviewed above suffer from the disadvantage of having limited samples with which to work and the results of these studies must by necessity be treated with some caution because of this. Of course a researcher can only ever work with the material available and this is a problem endemic to all studies involving fossil hominids.

An alternative hypothesis explains the differences in body size and morphology between the Neandertals and the early and later modern human populations of Europe and Western Asia, as being based on functional principles due to behavioural (cultural) changes in activity patterns and tool use (Verneau 1906) cited in (Holliday 1999a: 550; Biasutti 1951; Brues 1959: 466; Wolpoff 1995, 1989, 1992: 682-684; Caspari 1992; Frayer 1980, 1981, 1984; Trinkaus 1983, 1984, Trinkaus & Zimmerman 1982: 268-270). Holliday and Falsetti (1995) have tested the competing hypotheses of "climate" vs "mobility" using data from 19 recent "forager" groups. They compared the values for relative sitting height (alternatively relative leg length) with the "mobility" values of home range size and the number and distance of residential moves per year and the climate variables of effective temperature, precipitation and latitude (Holliday & Falsetti 1995: 144). The mobility and climate data were subjected to principal component analysis and the resulting scores for each group were correlated with the values for relative sitting height (Holliday & Falsetti 1995: 145). No significant correlations were found between the mobility components and relative sitting height, but there was a significant correlation between PC2 climate (precipitation) and relative sitting height, but not with temperature (PC1). A partial correlation analysis, holding climate constant, did not reveal any hidden relationship between limb length and mobility (Holliday & Falsetti 1995: 145-149). They suggest that these results reject the mobility hypothesis but fail to reject the climate hypothesis (Holliday & Falsetti 1995: 149). This conclusion is not particularly strong because of the unexpected result with regard to climate (Holliday & Falsetti 1995: 150). It should also be noted that the authors use of PCA with small samples sizes, a low variable to sample size ratio and the use of variables with non-normal distributions further weaken their results.

Because human thermoregulatory physiology suggests a tropical origin (Weiner 1973), researchers have looked further back in time for the effects of climatic selection, and many of the unique features of hominids such as the upright stance, lack of body hair and the predominance of eccrine sweat glands have been linked to the necessity to stay cool (references below). Perhaps the most prolific writer on this subject has been Wheeler (1984, 1985, 1991a, 1991b, 1992a, 1992b, 1993). Of particular interest to this thesis are his papers that link thermoregulation to the evolution of human body size and shape. Wheeler's thesis was that an upright stance reduced the proportion of the body that was exposed to the sun, particularly at midday (Wheeler 1985). It also raised the body above the thermal boundary layer of the land surface where daytime heat is highest and wind-speed lowest (the higher off the ground the cooler and windier it gets) thereby increasing the effectiveness of convective heat loss (Wheeler 1991b). The large number and high

density of eccrine sweat glands on the upper body and scalp also increased the effectiveness of convective and evaporative cooling (Porter 1993; Wheeler 1991b: 418). The trend for larger body size from *Australopithecus* to *Homo*, Wheeler contended, was linked to water conservation - a larger body dehydrating more slowly than a smaller body - thus loosening the ties to water sources and allowing hominids to forage over larger territories (Wheeler 1992a): 357-359). He noted, however, that the advantage of larger body size had an upper limit of about 80kg. An increase in linearity (tall and narrow) would have conferred a greater advantage, as it raised "the body even further above the ground, thereby facilitating convective heat loss and providing a larger total area for heat dissipation without increasing exposure to the strongest fluxes of direct solar radiation experienced when the sun is at high elevations" (Wheeler 1992a: 356-357; see also Wheeler 1993).

Over several papers Ruff has examined the variation in body morphology in fossil hominids and the possible role of climate in this variation (Ruff 1991, 1993, 1994; Ruff & Walker 1993). Of particular interest to Ruff was the difference in relative pelvic breadth between the small, but broad-bodied hominids such as *Australopithecus afarensis* (eg. AL 288-1) and the larger but narrower-bodied hominids typified by *Homo erectus*/*Homo ergaster* (eg. KNM-WT 15000). Despite the relative difference, AL 288-1's pelvic breadth is only 2cm greater than the estimate for the adult breadth for KNM WT-15000 and is in the middle of the range for living Africans (Ruff 1991: 87, Table 1).

To explain this, Ruff turned to the thermoregulatory principles based on Bergmann's and Allen's rules that link heat conservation/dispersion to surface area to weight (or mass) ratio. Ruff likened the human body to a cylinder, with stature representing cylinder height and bi-iliac breadth the cylinder diameter (Ruff 1991: 83). He found that by using the "equations for a cylinder, it can be demonstrated that *in order to maintain SA/M ratio with changes in height, breadth must remain constant*" (Ruff's emphasis) (Ruff 1991: 82)(see Figure 3.3 in Section 3.3.2.2, above). Therefore the SA/W ratio of a cylinder is dependent on its diameter, not its length.

To support his thesis Ruff examined the variation in bi-iliac breadth in recent humans and found that there were clear geographic differences in absolute bi-iliac breadth between populations, with Africans having the narrowest hips and northern Asians having the widest (Ruff 1991: 87). This difference, Ruff argued, was linked to climate. Roberts had previously demonstrated a large and very highly significant negative correlation between temperature and relative bi-iliac breadth ( $r = -0.823$ ) (Roberts 1973) and, indeed, this was the highest correlation Roberts achieved between his climate and body variables. Ruff, using his own sample set, calculated a correlation between latitude and absolute bi-iliac breadth of  $r = 0.895$  for males, and  $r = 0.919$  for females, both very highly significant at  $p < 0.001$  (Ruff 1991: 86). Ruff compared the fossil hominids that preserved enough of a pelvis for analysis (AL 288-1: *A. afarensis*, STS 14: *A. africanus*,

KNM-WT 15000: *H. erectus* and Kebara: *H. sapiens neanderthalensis*) with recent humans. He demonstrated that whilst the two small-bodied hominids were relatively very wide and the large bodied *H. erectus* was relatively very narrow, this was due to variation in stature not body breadth: indeed as mentioned above, their absolute body breadths are in line with recent human populations living in low latitudes (Ruff 1991: 89). The Neandertal, meanwhile, although having a relative body breadth in line with northern Asian and some European groups, was absolutely wider than any of the mean bi-iliac breadths of these groups (although it was within the range of individual values) (Ruff 1991: 89-90) (Figure 3.11). Ruff concluded that "similarities or differences among fossil and living hominids in relative body breadth may in part simply reflect allometric constraints to maintain physiological equivalence, i.e. homeothermy, at different body sizes" (Ruff 1991: 90).

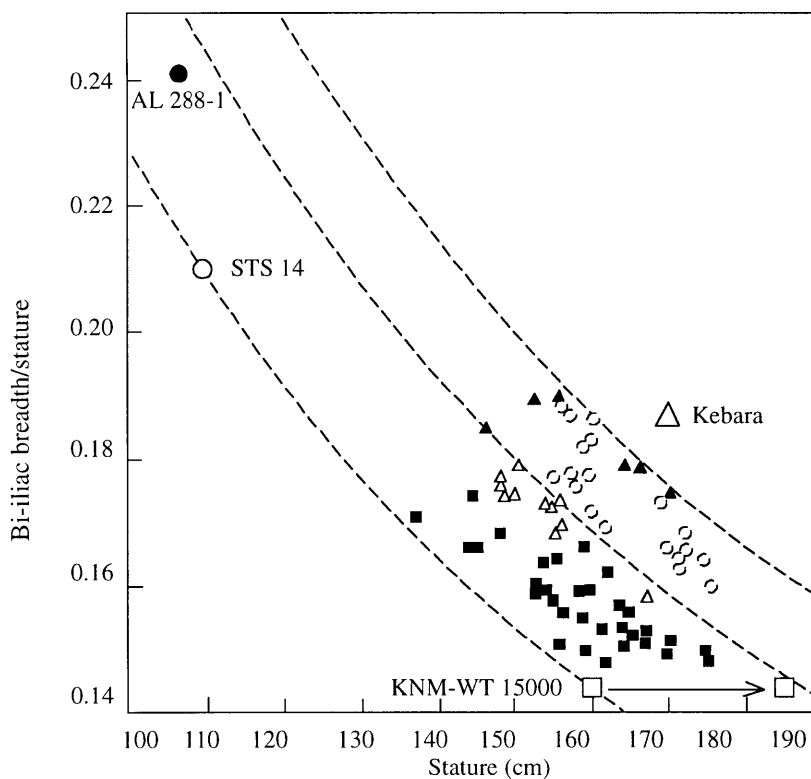


Figure 3.11: Relative body linearity vs stature, reproduced from Ruff 1991: 89.

Extending his analysis to include early modern humans from Europe, Ruff found that in terms of body width/femur length and estimated weight for height, they tended to fall, when plotted, between the low and high latitude recent human groups. Ruff interpreted this to mean that these early modern *H. sapiens* had an "intermediate body shape" adapted to a warm temperate climate or were in the process of evolving from a heat adapted state towards a more cold adapted one (Ruff 1994: 82-86). The situation for relative limb lengths was somewhat different. While the early moderns were intermediate in terms of

the relationship between tibia length and femur length, Ruff found no evidence of ecogeographic patterning in the relative limb lengths of the early moderns (and Neandertals) of Europe and Southwest Asia as would be predicted by Allen's rule. In contrast, the relationship between femur length to femoral head breadth indicated that the Southwest Asian groups (both Neandertal and early modern) had longer femurs compared to femoral head size (that is, were more like tropical populations) than the European groups (Ruff 1994: 86-90). He concluded that researchers should be cautious of attempts to extrapolate "body morphology between geographic regions and in reconstructing body size and shape in fossil hominids without considering the potential effects of climatic adaptation on body form" (Ruff 1994: 102). An example of this approach can be found in a number of papers by Trinkaus, Ruff and colleagues when analysing limb morphology of fossil hominids (Trinkaus 1997, 1999; Trinkaus *et al.* 1999b, Trinkaus & Ruff 1999; Trinkaus *et al.* 1998a; Trinkaus *et al.* 1998b; Trinkaus *et al.* 1999c; Trinkaus *et al.* 1999a; see also the paper on Lagar Velho 1, Duarte *et al.* 1999).

Finally another area of interest to this thesis is the role played by climate in the evolution of human nose shape. Correlations between climate and nasal shape have been reviewed in Section 3.3.4.4 and reveal clear associations between nasal size and shape and climate. The situation has also been examined in fossil hominids. As mentioned above, the Neandertal nose has long been argued to be an adaptation to a cold, dry climate: its shape and size important to warming inspired air and its extreme anterior position also thought to help insulate the brain from the cold (Coon 1962: 534; Brose & Wolpoff 1971: 1178; Wolpoff 1995: 677; 681-682). Franciscus has also suggested that the large nasal aperture could aid in capturing moisture from expired air and enhance "dissipation of excess heat in arid and cold/arid conditions in the context of regularly elevated activity levels..." (Franciscus 1989: 223). Indeed, the very appearance of a prominent and more voluminous external nose in *H. erectus* has led Franciscus and Trinkaus to argue that this was brought about by the need to reduce moisture loss through the respiratory system due to a change in activity patterns including increased diurnal foraging in open semi-arid country (Franciscus and Trinkaus 1988: 525). This hypothesis is supported by other morphological changes that indicate adaptation to hot/dry conditions in *Homo erectus* (Franciscus and Trinkaus 1988: 525).

### 3.4 SUMMARY OF SECTION 2

Section 2 "Context" was presented in two chapters. Chapter 2 dealt with the environmental, archaeological, historical and evolutionary contexts of the analysis. Chapter 3 began with a review of the work of Joseph Birdsell in order to provide a context to the data used in this analysis. It also provides an area of potential discussion, in particular, Birdsell's hypothesis that there were geographically and morphologically

distinct populations of Aborigines who represented the remnants of three distinct waves of human migration into Australia.

Above all this chapter has revealed the broad scope of the relevant literature on the topic of ecogeographic correlations. Its breadth is due to the complexity of the issue, touching as it does upon aspects of evolution in general and, more specifically, the way in which both invertebrate and vertebrate animal species maintain thermal balance through physiological and morphology adaptations. It has also become important to questions regarding the evolution of the hominid line and to the appearance of modern humans. As can be seen in the review above, the discussion of the rules of Bergmann and Allen has produced far more controversy when applied to humans than to any other animal. Much of the controversy would seem to reflect an historical bias that considers humans a special case when it comes to evolution.

There are many observational and experimental studies on the existence or otherwise of Bergmann's and Allen's rules in the literature. Many studies have confirmed the existence of Bergmann-like size clines but the nature of these clines is still debated. Experimental studies have indicated that animals exposed to heat or cold during growth demonstrate a range of plastic developmental responses that might explain an aspect of the size and shape clines observed by Bergmann and Allen. When grown in cold conditions animals achieved a greater final body size and weight and relatively shorter limbs than the controls, and those exposed to heat tended to be smaller, lighter and have relatively longer limbs. Studies have also shown that larger, stockier-bodied rats live longer in extreme cold than more linear rats and vice versa.

Observational studies relating human body form to climate have repeatedly found that a stocky body form is found in populations living in cold climates and a more linear form in hot climates. However, the issue of the relationship between body size and climate (Bergmann's rule *sensu stricto*) in humans is less clear. Part of the problem hinges on whether body size is measured as weight or stature. Although significant correlations between weight and temperature and stature and temperature exist they are variable in strength (and sometimes in direction) particularly within geo-ethnic groups, and special pleading has been made to explain the findings of some studies.

Other studies, both observational and experimental, have confirmed that certain human body types are better suited to particular climatic conditions; however they have also revealed that humans possess the ability to significantly adapt to different climatic regimes either through developmental plasticity or through short-term physiological changes. These adaptations, however, are complicated by other important and sometimes interrelated factors such as culture, disease and nutrition.

Despite a number of vehement critics of Bergmann's and Allen's rules, especially as they apply to humans, the overall consensus would appear to be that the repeated

observance of these ecogeographic clines across many animal species, including humans, suggest that they are not coincidences and that they represent some form of response to aspects of climate. Whether this is a response to a direct or indirect aspect of climate is, however, still a matter of debate.

Climate has also been implicated in the geographic variation of the human cranium and face and in particular the nose. Early ecogeographic studies revealed that noses tended to be higher and narrower where the average temperature was colder and the air drier. This was argued to be an adaptation for warming and moistening the air in the respiratory passages prior to its entry into the lung. An alternative explanation also linked ecogeographic correlations of nose shape to the need to reduce moisture loss from the lungs. A number of studies have examined the distribution of nose height, breadth and protrusion as well as sinus volumes, however the hypothesis that the nose has an important air-conditioning function has apparently never been tested experimentally in humans.

It has also been suggested that the entire face could be under climatic selection with Coon arguing that the Mongoloid face was adapted to minimise cold injury. This hypothesis, however, has been discounted through the experimental work of Steegmann.

The cranium too has been investigated in relation to ecogeographic adaptations. Beals has hypothesised that a larger and more brachycephalic skull is adaptive to cold temperatures, as a larger and rounder head has a lower surface area to volume ratio and thus is better at retaining heat. Beals did find some evidence for ecogeographic clines in head size and shape in modern humans, but could not find strong evidence that these traits varied in hominids in response to the temperature changes of the Pleistocene. As well, the progressive trend towards brachycephalisation over the last eight centuries of the Holocene, when average temperatures have been similar to those of the present, also casts doubt on the whether climate is an important factor in the geographic variation of head size and shape.

The final part of the chapter reviews studies that have used an ecogeographic framework to elucidate the problem of modern human origins and the fate of the Neandertals in Europe and Southwest Asia. Adding to the well known differences in cranio-facial anatomy between Neandertals and modern humans, these studies have revealed interesting discontinuities in body shape between these groups that would seem to indicate that they were adapted to very different habitats and life-ways. This evidence has been used to support the contention that humans adapted to a warm climate migrated into the Near East and Europe, finally absorbing or, perhaps, replacing the Neandertals.

Perhaps the most important contribution of these studies is to provide researchers with a way of allowing for microevolution when considering the macro-evolutionary aspects of hominid phylogeny.

**SECTION III**

**MATERIALS**

**and**

**METHODS**

# CHAPTER 4

## MATERIALS

### 4.1 INTRODUCTION

This chapter will detail and discuss the materials to be used in the analysis. There are two main elements to the database: climate data and measurements of human morphology. The latter primarily consist of anthropometric measurements of living subjects. There is also a smaller sample of osteometric measurements of limb lengths.

### 4.2 ENVIRONMENTAL DATA

#### 4.2.1. Australian Climate Data

The climate data for Australia were drawn from the 1975 edition of "Climatic Averages, Australia" produced by the Australian Bureau of Meteorology. The time depths of these data were variable. At some stations recordings of temperature and humidity go back only 15 to 17 years, however at other stations rainfall data have been collected for over 70 years. Temperature (Dry Bulb) was:

"registered by a mercury-in-glass thermometer exposed in a white louvered box, known as a Stevenson screen, which allows the air to circulate slowly through it. Temperatures measured in this way are also referred to as shade temperatures" (Bureau of Meteorology 1975: vi).

Relative humidity was calculated from dry and wet-bulb temperatures (Bureau of Meteorology, 1975: vii). The units of measurement are degrees Celsius for temperature and millimetres for rainfall (Bureau of Meteorology, 1975: v).

#### 4.2.2 World Climate Data

In Chapter 9, anthropometric measurements from a worldwide sample of human populations are correlated against climate variables. Climate data for this analysis were taken from the "World Survey of Climatology" series (Arakawa 1969; Bryson & Hare 1974; Gentilli 1971; Griffiths 1972; Schwerdtfeger 1976; Takahashi & Arakawa 1981; Van Loon 1984; Wallén 1970; Wallén 1977). This contained a similar range of data for all geographic regions, although not every measurement was available from all weather stations: in particular data for relative humidity were often not available.



### 4.2.3 Criteria for the Selection of Climate Variables.

1. **Access to data.** Given that doctoral research is constrained both by time and money, the ease of access to data is paramount. Luckily climate data are readily available, although the most accessible long-term data are usually not the most up-to-date. However, given that Birdsell's data were collected no later than the mid-1900s, more up-to-date data are unnecessary.

2. **Location of weather stations.** The weather stations from which data were taken were as close as possible to the centres of the population sample areas (sample areas are illustrated in Figure 4.3). Where there was no weather station inside an area, the closest station at a similar latitude and altitude was chosen. Details and locations of the weather stations are presented in Appendix 1.

3. **Precedent.** Climate variables were chosen primarily because they had been used in previous research and were either identical, or the closest measurement, to those used in other studies (see Chapter 3). In this way the results of the present study were comparable to earlier research. However, whether or not these are the most appropriate measures to use in an ecogeographic analysis is entirely another question, and this will be pursued in later chapters.

4. **Selective importance.** It has been unclear to researchers which climatic factor has the greatest selective effect on animal populations. Bergmann's and Allen's rules refer only to temperature, but many environments, especially those away from the tropics are subject to seasonal extremes of heat and cold, rain and drought. Even much of the tropics have extreme diurnal and seasonal fluctuations in climate. Organisms exist in complex environments and must adapt in complex ways. Therefore a spread of climatic variables was chosen in order to assess this complexity.

### 4.2.4 Climate Variables

Originally eleven climate variables were chosen and these were reduced to eight as bivariate correlations indicated that some of these variables were redundant. The original climate variables included:

1. Mean maximum temperature of the hottest month (°C) (Max Hot; Hottest Month),
2. Mean annual maximum temperature (°C),
3. Mean minimum temperature of the coldest month (°C) (Min Cold; Coldest Month),
4. Mean annual minimum temperature (°C),
5. Relative humidity of the most humid month 9am (%) (RH Wet; Most Humid

- Month),
6. Relative humidity of the least humid month 3pm (%) (RH Dry; Least Humid Month),
  7. Annual variation in temperature (°C) (Ann Temp Var; Temperature Range),
  8. Annual variation in relative humidity (Ann RH Var; Humidity Range),
  9. Average annual temperature (°C) (Av Ann Temp; Annual Temperature),
  10. Average annual relative humidity (%),
  11. Average annual rainfall (mm) (Ann Rain; Annual Rainfall).

The two location variables of latitude and longitude will also be used in the analysis.

Hereafter, these variables will be referred to in the results tables by the first abbreviation in brackets, and in the text, by the second abbreviation. Those without an abbreviation were dropped from the analysis.

Of these variables, Hottest Month, Coldest Month, Most Humid Month, Least Humid Month and Annual Rainfall are direct measurements as recorded at the weather stations. The remaining three are calculated from recorded measurements:

1. Annual variation in temperature (Temperature Range) = Hottest Month - Coldest Month
2. Annual variation in relative humidity (Humidity Range) = Most Humid Month - Least Humid Month
3. Average Annual Temperature (Annual Temperature) = 
$$\frac{\text{mean annual maximum temperature} + \text{mean annual minimum temperature}}{2}$$

## 4.3 MORPHOMETRIC DATA

### 4.3.1 Anthropometry

#### 4.3.1.1 Birdsell's Australians

##### Sampling

The population sample used in this analysis includes 1424 adult males and 880 adult females of exclusive Aboriginal ancestry. Adulthood was taken to be 20 years for males and 18 years for females corresponding roughly to skeletal maturity (Krogman & Iscan, 1986). The American anthropologist Joseph Birdsell recorded these data during two expeditions to Australia. The first was the Harvard - Adelaide University expedition of

1938 - 1939 (designated "N" in the Adelaide University series of expeditions). The second was the U.C.L.A. - Adelaide University, "R", expedition of 1952 - 1954 (Birdsell 1941, 1949, 1967, 1977, 1993; Tindale and Birdsell 1941). During these expeditions Birdsell and his major collaborator Norman Tindale, of the South Australian Museum, recorded a range of demographic data, metrical measurements, morphological traits and serological data of Aboriginal people from a large expanse of Australia.

The sampling strategy used by Birdsell, and followed in this analysis, is frankly opportunistic. Whatever data were available have been used with some minor exceptions. These exceptions included the rejection of individuals deemed juvenile and of groups with fewer than five individuals. The lower limit of five is an arbitrary cut-off; however it was set at this level as it is highly debatable that such a very small sample can adequately estimate the parameters of the theoretical population from which it was drawn. The inclusion of groups of small size (between 5 and 10 individuals) was justified in order to maximise the area of Australia covered by the analysis. As can be seen in Table 4.1, small sample sizes occur rarely in the male sample, but are more common in the female sample.

The majority of the analysis will utilise Birdsell's data exclusively. There are other anthropometric data available for Australia, however as noted below in Section 5.3, some measurements from these observers are not strictly comparable with those of Birdsell's. As a result, these other data will only be used in the world sample analysis and will not be used to calculate correlation coefficients for Australia alone. Measurements that are clearly not comparable will not be used. In this way inter-observer error can be eliminated from the analysis of Australian data and controlled for in the world sample. Intra-observer variation is, of course, still a potential source of error. It can be assessed for Birdsell's measurements (see below, Section 5.3.3.1), but remains unknown for the data from other sources.

Birdsell had initially divided his "N" expedition groups into 25 regions (B1 - B25), however B25 was later dropped and incorporated into other regions (Figure 4.1). These areas were divided on a geo-cultural basis and contained individuals from more than one tribe. The "R" expedition series was divided into twenty-eight large groups (or tribes: T-1 - T-28); two small tribes: T-A and T-B, and seven regions: P-A to P-G (Figure 4.2), which contained individuals from a number of tribes. Several tribal groups were sampled during both expeditions and were later pooled together by Birdsell (Birdsell 1993). These were the Mandjindja, areas B6 and T9, the Nyanganyatjara, areas B5 and T11, and the Ngatatjara, areas B7 and T13.

For the purposes of this analysis Birdsell's two series were amalgamated and the groups given individual number designations (Groups 1 - 60, male and 61 - 120, female) (see Figure 4.3 where the group areas are identified by the male sample group numbers).

All of Birdsell's sample groups are listed in Table 4.1, however not all groups will appear in the analysis. Areas B5, B6 and B7 (Groups 5/65, 6/66 and 7/67) were tribes sampled in both expeditions and were pooled into Areas T11 (Group 36/96), T9 (Group 34/94) and T13 (Group 38/98) respectively. The areas B3 and PF were pooled into Group 3/63 as were B8 and PG into Group 8/68. As mentioned above areas with less than five individuals have not been included. This has resulted in 57 male groups and 45 female groups from Birdsell's database to be included in further analysis.

In Table 4.1 the column titled "Sampling" refers to how many tribes were sampled from those recorded to be extant or extinct in the sample area. For example, 4/7, is four tribes sampled out of seven. These data are taken directly from Birdsell (1993), however the numbers and names of the tribes taken from Birdsell's original data cards differ somewhat from those published in his monograph.

On his method of choosing sample areas and sample sizes for his first expedition Birdsell records that:

"In order to obtain a geographical distribution of traits, Australia has been divided into 25 areas. An attempt has been made to divide the series of 578 aborigines so as to have minimum of 20 full bloods for each area. Unfortunately, 7 of these areas contain less than this number. The allocation of areas has been based primarily upon the clustering of tribal groups within the data available in our own series, with physiographic considerations being utilised as delimiting factors. The areas have, where possible, been drawn to make the contained physical type as homogeneous as possible. Boundaries have been determined in detail in some cases by subsidiary data such as linguistic and cultural factors.

Assignment of individuals to these geographic or tribal areas has been largely on a purely tribal basis, but in a certain number of cases, especially in the old settled areas, locality assignments have been made in those cases in which tribal affiliation is not remembered. Thus the birthplace of parents, or in extreme cases, of the individual himself, have determined the area. In a number of cases the tribes of parents belong to separate but adjoining areas. In these cases random assignment to the areas has been made on the basis of series numbers, odd sequence numbers being thrown into the area containing the fewer individuals" (Birdsell 1941: 25).

The sample numbers, and thus the mean values for anthropometric variables in this analysis, vary slightly from those published by Birdsell in 1993. One reason for this is that the data were taken from his original data cards, a few of which were missing. Birdsell's criterion for subject inclusion based on age was also slightly different to mine. In cases

where individuals did not know their birth-date, both Birdsell and Tindale estimated age through observation and questioning. This often resulted in a wide-ranging estimate of age which included upper and lower values (eg. 25 - 30 or 35 - 40). I was more inclined to use the lower estimate of age and Birdsell the upper estimate. This might mean that a male estimated to be between 18-20 would be included by Birdsell but excluded by me. Overall, however, the difference in sample number and mean values for variables is slight.

### **Tribal Names**

Over the years tribal names have changed, due either to a misunderstanding of pronunciation and transcription into roman script, misinformation from neighbouring tribes, or confusion over section, sub-section, moiety or clan names versus tribal names. This is covered in some detail in Tindale (1974) which contains a list of the various alternative names attributed to Aboriginal tribes. Where spellings have changed since those published in Birdsell (1993) they have been updated with the newer versions taken from the map of "Aboriginal Australia" by David Horton (Horton 1996). Another factor in this confusion over names is that since Birdsell and Tindale conducted their expeditions, some tribes have amalgamated, and what were once groups with separate identities, now consider themselves to be part of a larger grouping. For instance, the Ngalia are now identified with the Warlpiri, and the Kartudjara, Mandjildjara and Wanman have amalgamated with the Mardu. A number of the smaller tribes in the rainforest region of north Queensland have also amalgamated (Horton 1996).

In Table 4.1 the first "tribal" name listed is that found on the data cards, or as published by Birdsell; those in brackets are either a revised spelling, or the most recent 'tribal' name accepted by a particular group. A question mark denotes a name that could not be located on the map of "Aboriginal Australia" (Horton 1996), or an alternate spelling of which I was uncertain.

The term "tribe", itself, is the centre of debate amongst anthropologists. The main objection to the term is that it is a western view of Aboriginal society, particularly in terms of how individuals and groups are connected to their land via religion and economy. This is not the place for a discourse on the complexity of Aboriginal land tenure or cosmology, however as Berndt and Berndt (1977) point out, the term "tribe" is usually used to define a group that share a territory, language and/or dialect and a common culture and mythology. Birdsell referred to this as the "dialect tribe" that "consisted of a cluster of related and contiguous bands, who spoke a common dialect, and had a generally uniform cultural inventory" (Birdsell 1993: 7). More importantly it is a grouping that the members see themselves as belonging to, in contrast to other groups or outsiders. The term does not refer, however, to either a political or economic unit, and may not have a sharply defined boundary.

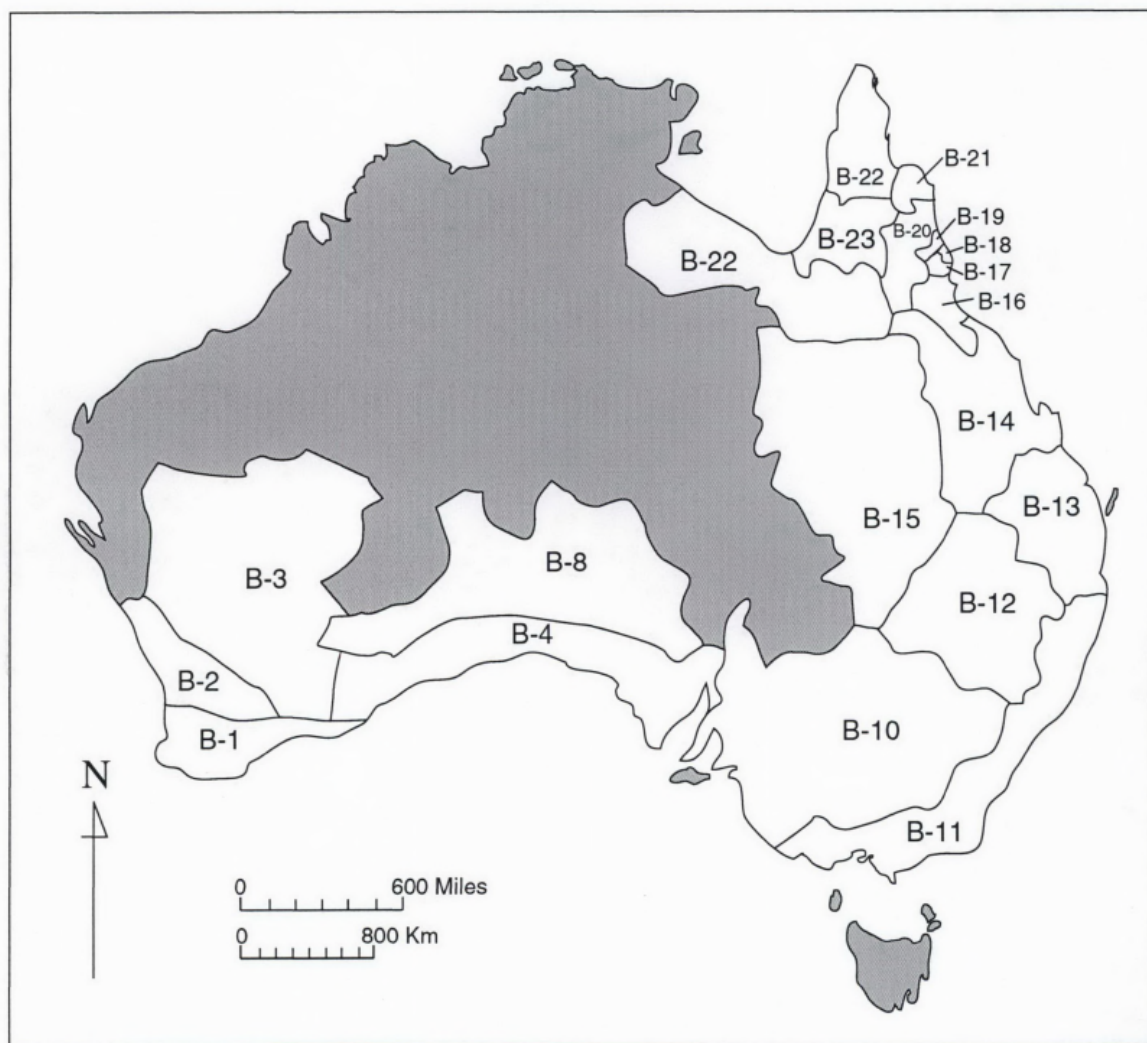


Figure 4.1: Map of areas sampled during Expedition N, adapted from Birdsell, 1993: 25. Areas for B5, B6 and B7 are as for T11, T9 and T13 respectively, as shown on Figure 4.2.

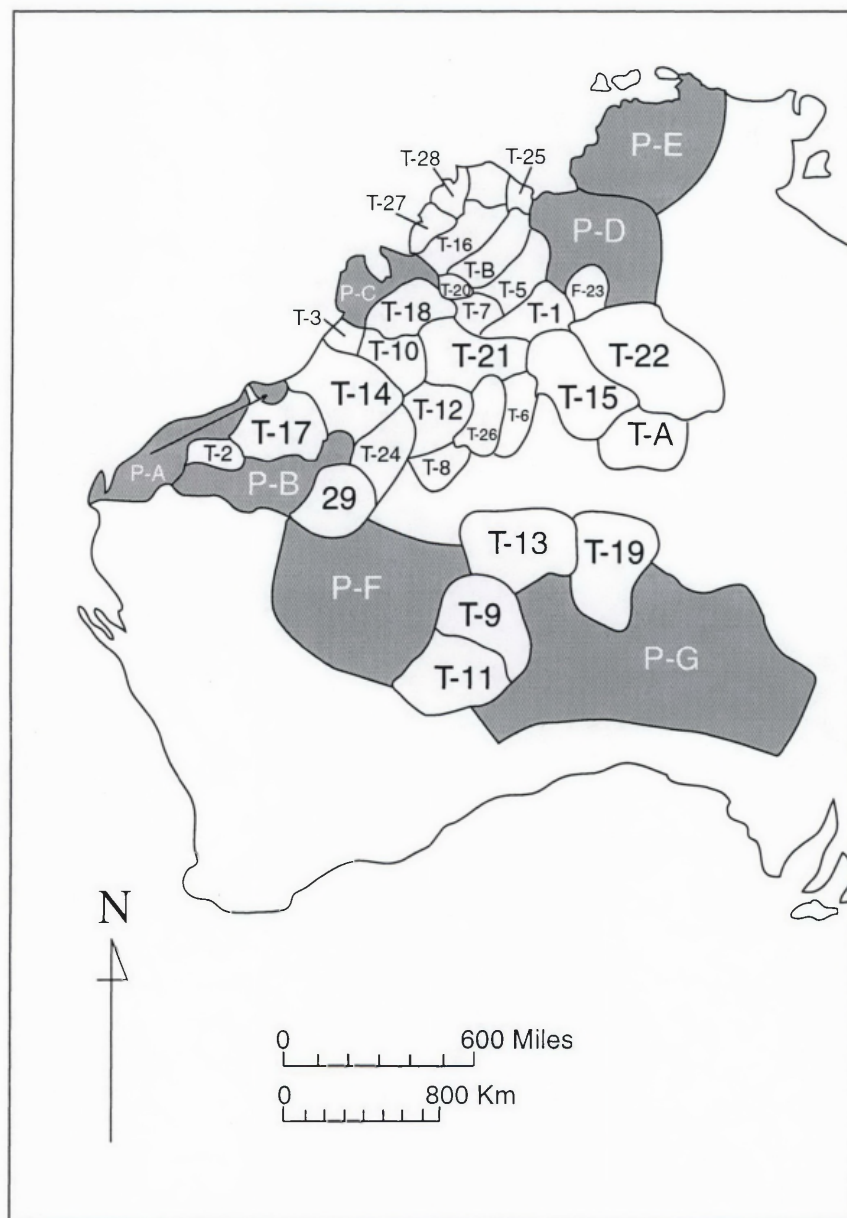


Figure 4.2: Map of areas sampled during Expedition R, adapted from Birdsell, 1993: 10.

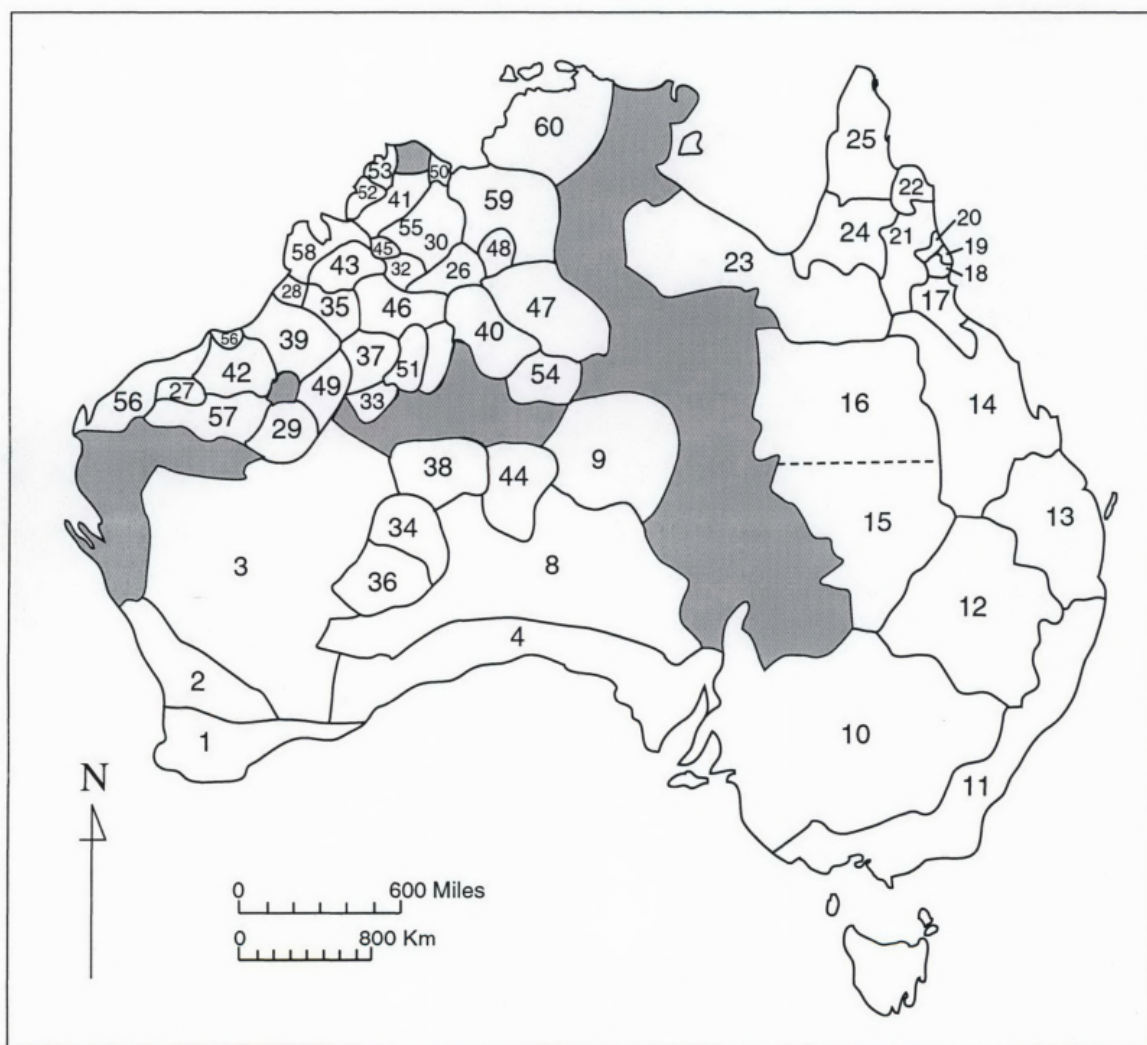


Figure 4.3: Map of sample areas used in this analysis.



Table 4.1: Birdsell's Australians

Area	Group No. M/F	Area Name	Tribal Affiliation	Sampling	N
B1	1 / 61	Southwest Coast	Njunga (Wudjari), Koreng (Goreng), Kaneang (Kaniyong), Minang,	4/7	m = 25, f = 15
B2	2 / 62	Southwest Hinterland	Unknown	?/6	m = 14, f = 6
B3/ PF	3 / 63	Southwest Interior and Canning Route	Kalamaia (Kalaamaya), Koara (Kuwarra), Koarawonga (Kuwarra?) Nana, Pini (Nana), Mardo (Mardu), Wangkathaa, Wadjeri (Watjarri), Targadi (Thargari ?)	7/10	m = 28, f = 11
B4	4 / 64	South Coast	Ngadjunmaia (Ngatjumay), Wirangu, Mirning, Pankala (Banggala), Nukuna (Nukunu)	4/6	m = 22, f = 21
B8/ PG	8 / 68	Southern Hinterland	Kokata (Kokatha), Tjararidjari (Nyanganyatjara), Nangaa (Nyanganyatjara), Ngalea, Kuyani, Sandhill Pitjantjatjara, Antakarinja, Jangkundjara (Yankuntjatjara)	6/8?	m = 51, f = 25
B9	9 / 69	Central Interior	Aranda (Arrente), Southern Aranda (Arrente), Warumungu Walpiri (Warpiri)	?	m = 9, f = 1
B10	10 / 70	Murray Drainage (mostly lower R. Murray)	Tanganekald (Ngarrindjeri), Jarildekald (Ngarrindjeri) Maraura (Barkindji), Barkindji, Wemba-Wemba, Latjalatji (Latje Latje), Wongaibon, Bunandaity ?	8/54	m = 21, f = 7
B11	11 / 71	Southeast Coast	Kurnai, Kitabal (Bundjalung), Juing (Yuin), Bidawal (Bidwell), Djaingadi (Dainggatti), Kumbainggiri (Gumbainggir)	5/46	m = 23, f = 7
B12	12 / 72	Darling Drainage	Kunggari (Gunggari), Koamu (Kooma), Kamilaroi	7/17	m = 28, f = 5
B13	13 / 73	East Coast	Darambal (Darumbal), Kangulu (Gangulu), Korongorong (Gureng Gureng), Batjara (Badjala) Jimon (Yiman), Jagora (Yuggera), Waka Waka Kabikabi (Gubi Gubi)	11/27	m = 22, f = 4
B14	14 / 74	Northeast Coast	Bira (Biri), Ngaro (Giya?), Widi (Wangaa), Kairi (Gayiri), Bindal, (Barada) Baradha, Karinbal (Garingbal), Wadja (Wadjigu?), Pitjara (Bidjara), Wadjaingo (Wadjigu) Jagalinga (Yagalingu)	9/23	m = 21, f = 5
B15a	15 / 75	Eastern Interior 1 (South)	Badjiri (Budjari), Kalali (Kullilla), Marangangi (Margany) Dieri, Wanjiwalka (Wanjiwalgu), Kungna (Kunja), Wadjalan (Dharawala), Karuwali, Kungari (Kuungkari)	12/30 Between 15Aand15B	m = 20, f = 3

Table 4.1: Birdsell's Australians

Area	Group No. M/F	Area Name	Tribal Affiliation	Sampling	N
B15b	16 / 76	Eastern Interior 2 (North)	Jirandli (Yirandali), Kalkadun (Kalkadoon), Maithakari (Maya Thakurti?), Koa (Guwa), Jalana (Yalarrnga)		m = 8, f = 2
B16	17 / 77	Cardwell Region	Keramai (Djirbalngan), Warakamia (Nyawaygi), Njawagi (Nyawaygi), Wukurukaba?, Wagamai?	4/7	m = 18, f = 3
B17	18 / 78	Ravenshoe Region	Djirubal (Djirbalngan?), Mamu (Djirbalngan), Ngatjan (Djirbalngan), Gulnai (Djirbalngan), Bijai?	5/5	m = 33, f = 4
B18	19 / 79	Cairns Area	Idindji (Yidinjdji), Kongkandji?, Wanjuru?, Tjapukandji(Djapugandjji?)	3/4	m = 31, f = 16
B19	20 / 80	Kuranda Region	Tjapukai (Djapugandjji?), Tjapukandji(Djapugandjji?)	3/3	m = 31, f = 27
B20	21 / 81	Upper Mitchell Drainage	Barbarum (Mbabaram)		
B20	21 / 81	Upper Mitchell Drainage	Muluridji (Kukuyalanji), Kokoelandji (Kukuyalanji), Kokopatan (Kukuyalanji), Gugu Badhun, Agwamin, Kokokulunger (Kukuyalanji), Djankan (Kukuyalanji)	9/12	m = 27, f = 13
B20	21 / 81	Upper Mitchell Drainage	KokoBididji (Kukuyalanji), Wargamaygan		
B21	22 / 82	Cooktown Region	Kokoimudji (Gugu-Yimidhirr), Kokowarra, Kokolamalama (Lamalama)	2/7	m = 20, f = 5
B22	23 / 83	Gulf of Carpentaria	Jokula (Ganggalida), Maikulan (Mayi Kulan), Tagalag (Takalak), Kotandji (Ngandji), Lardil, Karawa (Garawa), Wanji (Waanyi), Jangula (Yanuwa?), Kurtja?	12/21	m = 30, f = 3
B23	24 / 84	Lower Cape York	Kokomini, Kokoja (Kukatj?), Kukatji (Kurtja), Walangama	7/12	m = 26, f = 3
B24	25 / 85	Upper Cape York	Kandju (Kaantju), Kawadji (Uutaalnganu), Ombila (Umpila), Anamuti (Anggamudi), Pakadji (Kuuku-Ya'u), Wik, Olkolu (Kunjen), Winduwinda (Winda Winda), Barunguan (Kuuku-Yani)	10/44	m = 32, f = 1
T1	26 / 86	NA	Djaru (Jaru)	1/1	m = 61, f = 43
T2	27 / 87	NA	Indjibandi (Yindjibarndi)	1/1	m = 14, f = 17
T3	28 / 88	NA	Karadjara (Karrajari?)	1/1	m = 22, f = 19
T4	29 / 89	NA	Kartudjara (Mardu)	1/1	m = 14, f = 6
T5	30 / 90	NA	Kitja (Kija)	1/1	m = 37, f = 36
T6	31 / 91	NA	Kokatja (Kukatja)	1/1	m = 29, f = 22
T7	32 / 92	NA	Konejandi (Gooniyandi)	1/1	m = 7, f = 24
T8	33 / 93	NA	Mandjildjara (Mardu)	1/1	m = 28, f = 21
T9/B6	34 / 94	NA	Mandjinja	1/1	m = 47, f = 9

Table 4.1: Birdsell's Australians

Area	Group No. M/F	Area Name	Tribal Affiliation	Sampling	N
T10	35 / 95	NA	Mangala	1/1	m = 26, f = 27
T11/B5	36 / 96	NA	Nangatadjara (Nyanganyatjara)	1/1	m = 41, f = 19
T12	37 / 97	NA	Nangatara (Yulparitja)	1/1	m = 10, f = 11
T13/B7	38 / 98	NA	Ngadadjara (Ngatatjara)	1/1	m = 41, f = 30
T14	39 / 99	NA	Njangamarda (Nyangumarda)	1/1	m = 108, f = 71
T15	40 / 100	NA	Ngardi (Ngarti)	1/1	m = 18, f = 17
T16	41 / 101	NA	Ngarinjin (Narinyin)	1/1	m = 14, f = 15
T17	42 / 102	NA	Njamal (Nyamal)	1/1	m = 18, f = 17
T18/B25	43 / 103	NA	Njikenka (Nyikena)	1/1	m = 22, f = 16
T19	44 / 104	NA	Pitjandjara (Pitjantjatjara)	1/1	m = 12, f = 11
T20	45 / 105	NA	Punaba (Punuba)	1/1	m = 9, f = 16
T21	46 / 106	NA	Walmadjari (Walmatjarri)	1/1	m = 55, f = 46
T22	47 / 107	NA	Walpiri (Warlpiri)	1/1	m = 13, f = 7
T23	48 / 108	NA	Wandjira (Gurindji)	1/1	m = 19, f = 12
T24	49 / 109	NA	Wanman (Mardu)	1/1	m = 35, f = 46
T25	50 / 110	NA	Wemambal (Pintubi)	1/1	m = 31, f = 38
T26	51 / 111	NA	Wangkatjunga	1/1	m = 29, f = 26
T27	52 / 112	NA	Worora	1/1	m = 26, f = 27
T28	53 / 113	NA	Wunambal	1/1	m = 13, f = 15
T-A	54 / 114	NA	Ngalia (Warlpiri)	1/1	m = 9, f = 1
T-B	55 / 115	NA	Ola (Worla)	1/1	m = 7, f = 3
PA	56 / 116	Coastal Pilbara	Ngarla, Kariyara, Ngarluma, Talandji (Thalanyi)	4/8	m = 13, f = 15
PB/ B2b	57 / 117	Fortescue River	Bailgu (Palyku), Kurrama, Niabali (Palyku), Padjima (Banjima) Ngolibardu (Nyangumarda)	5/8	m = 18, f = 11
PC	58 / 118	Dampier Land	Baada (Bardi), Nyul Nyul, Waruwa (Warwa), Jawuru (Yawuru), Ongkomi (Unggumi), Nimanboro (Niamburu), Onkaring (Unggarangi)	6/10	m = 22, f = 19
PD	59 / 119	Victoria River	Malgin (Gurindji), Arnga?, Wardaman, Mudbarra, Miriwung (Miriwoong)	6/15	m = 6, f = 8
PE	60 / 120	Arnhem Land	Gunwinggu, Tiwi, Larrakia, Iwaidja, Wagait (Wadyiginy)	5/?	m = 10, f = 0

Of more importance to this analysis is whether the sample areas can be defined as reproductive units. Birdsell identified the dialect tribe as the major evolutionary unit in Aboriginal Australia, being largely endogamous, with most marriages (or matings) occurring within this unit, and only 12 to 14 percent of unions being extra-tribal (Birdsell 1958, 1993). Birdsell, however, found that after the social disruption caused by white settlement, extra-tribal marriages had increased in frequency and that the real precontact genetic differences between tribes must have been reduced by this (Birdsell 1993: 9). It can be seen that for the population samples used in this analysis those representing single dialect tribes can be considered breeding units with relatively little gene flow to surrounding units. The larger composite areas, however, can not be seen in this way, but would appear to be included in the larger regional groupings such as those proposed by Peterson (1976) and would represent the wider breeding unit: those that may include intertribal marriages.

#### 4.3.1.2 Other Australian Anthropometric Data

##### Adelaide University Expeditions

These data were recorded over about 15 years and in a number of separate expeditions under the auspices of Adelaide University and the Board for Anthropological Research of South Australia (Table 4.2). It consists of 355 males and 185 females distributed between 13 tribes (Figure 4.4). One group was discarded due to its very small size. Copies of these data cards were included in Birdsell's research collection housed at the South Australian Museum, Adelaide.

Table 4.2 : Adelaide University Expeditions

Expedition	Date	Place
A	1923*	Mt Eba
B	1926	Ooldea
C	1927	Macumber
D	1928	Koonibba
E	1929	Hermannsburg
F	1930	MacDonald Downs
G	1931	Cockatoo Creek
H	1932	Mt Liebig
I	1933	Mann Range, Ernabella
J	1934	Diamantina, Pandy Pandy
K	1935	Warburton Range
L	1936	The Granites
M	1937	Nepabunna
"SA Natives"	Various dates	Various Places

\* The data cards labelled 'A' in the Birdsell Archive do not concur on date and place with those recorded by Jones (1987). In this paper 'A' expedition was dated to 1925 and the place visited as Wilgena.

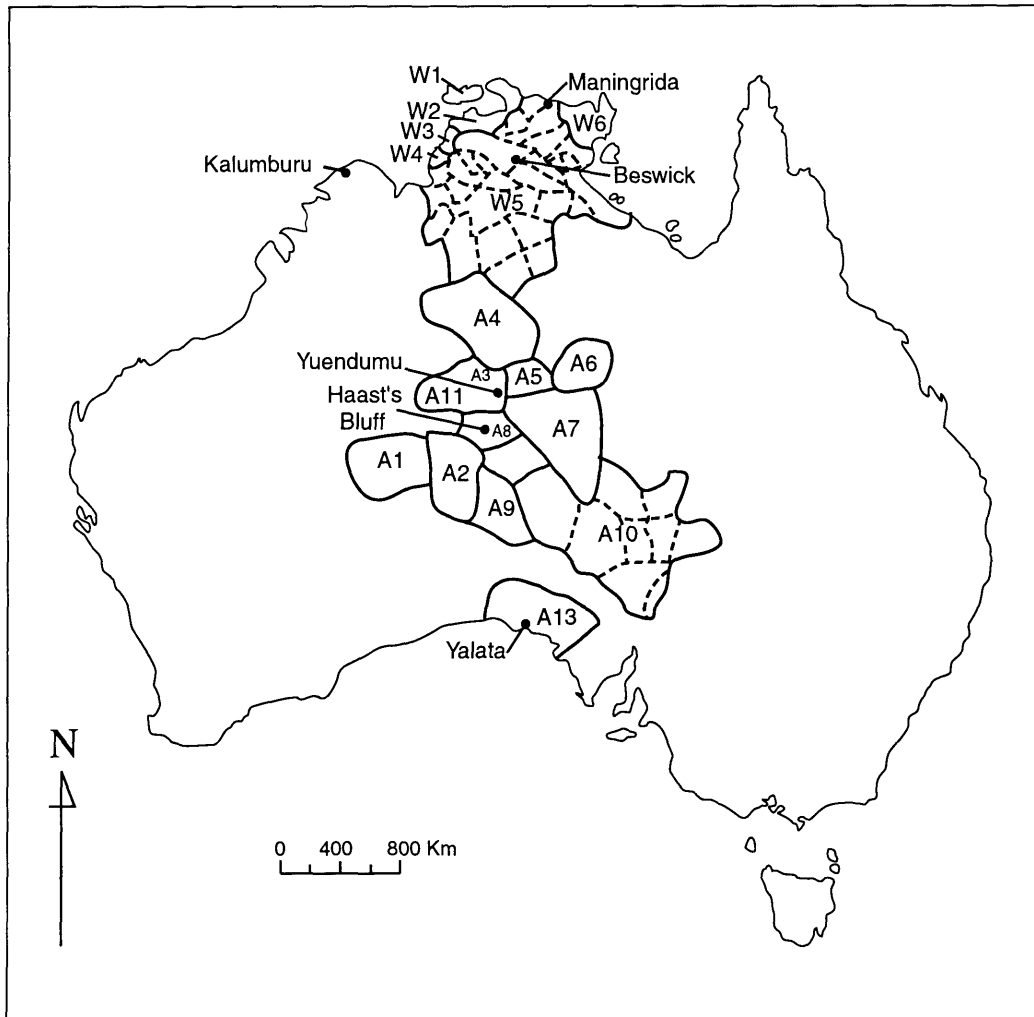


Figure 4.4: Map indicating the locations of Australian Aboriginal populations samples as measured by Adelaide University (A1-A13), Warner (W1-W6) and Abbie (●).

Table 4.3: Adelaide University Groups

JBB* Area	N M/F	Tribe/Region
A1	18/2	Ngadadjara
A2	52/25	Pitjandjara
A3	14/9	Ngalia
A4	27/6	Walpiri
A5	12/9	Anmatjera
A6	22/9	Ilaura
A7	72/23	Aranda
A8	41/22	Kokatja
A9	26/21	Jankundjara
A10	16/16	Wonkanguru
A11	7/8	Pintubi
A13	6/2	Wirangu

(\*As designated by Birdsell for his 1993 analysis)

These data represent the work of a number of different observers (see Jones, 1987: 87-88) and thus inter-observer measurement variation may provide a source of error. The individuals measured in these expeditions have been divided on a tribal basis as per the method of Birdsell (1993).

### Abbie

These data were collected by Andrew Abbie between 1951 and 1964 from groups living in the Kimberly (Kalumburu), Arnhem Land (Beswick and Maningrida), Central Australia (Yuendumu and Haast's Bluff) and South Australia (Yalata) (Table 4.4). The data were housed at the former Institute of Aboriginal and Islander Studies in Canberra, however this institution is now disbanded. Although Abbie's raw data are available to the author a problem has arisen because of the mixing of some the computer punch cards on which the data were recorded (Macho & Freedman 1987). As a result I have used the summary statistics published by Macho and Freedman (1987: 36-39, Table 4) who deleted cases with suspected mixed entries. The sample consists of 201 males and 150 females.

Table 4.4: Abbie's sample groups

Tribe/Region	N M/F
Kalumburu	28/26
Beswick	29/27
Maningrida	30/19
Yuendumu	24/18
Haast's Bluff	56/43
Yalata	34/17

## Warner

This is a series of 239 male adults mainly from northern Arnhem Land. It was collected by Lloyd Warner in 1927 at Port Darwin and Crocodile Islands and consists of men from Melville and Bathurst Islands, Northwest Arnhem Land, Northeast Arnhem Land, Victoria river (West) and Roper River (East) (Table 4.5). As Warner's main aim was to investigate the social organization of the tribes of this area, the anthropometric data were analysed and published by W.W. Howells (1937).

Table 4.5: Warner's Groups

JBB Area	N	Tribe/Region
W1	28	Melville Is and Bathurst Is
W2	20	Larrakia
W3	37	Worgait
W4	40	Magatige
W5	35	Central Interior
W6	77	Northeastern

### 4.3.1.3 World Samples

#### Introduction

A world sample is also to be analysed in this study for two main reasons. The first is to validate the methodology in a comparison with earlier studies, particularly those of Roberts (1953, 1973) and Katzmarzyk and Leonard (1998), where a similar range of data were used. The second is to compare the results from the intra-Australia population study, with those of a broader human sample. The main question being: do Bergmann's and Allen's rules apply to intra-regional populations in the same way as they apply to inter-regional samples? In this context, the term "region" refers to broad geo-ethnic groupings of populations such as European, Asian, African, Native American and so forth.

These data samples are drawn from various sources, and given this, the samples suffer from a lack of standardisation in the variables measured and, without doubt, in the technique of measurement. Thus there is a major possibility of inter-observer error. There is also a bias towards males, for as with many studies, data on males are more numerous than that on females. This discrepancy is particularly felt in the African sample with Hiernaux's compendium including males only.

The comparative world sample will comprise of body measurements only, as it was not possible to collect sufficient, comparable anthropometric data on cranio-facial variables.

## Europe and European Descendants

During his first expedition Birdsell measured a sample of what he termed "Old Australian Whites". These were individuals of mainly western European descent who were, at least, 2<sup>nd</sup> generation Australian. They were measured at Adelaide and consisted of a younger group of medical students and nurses, and an older group of males from a nursing home. The sample consists of 108 males and 84 females.

A number of other European samples was taken from data sources compiled by Eveleth and Tanner (1976). The details of these population samples can be found in that volume (1976: Appendix Tables 5a, 5b and 29).

## Sub-Saharan Africa

The data for African males are taken exclusively from the tables published in Hiernaux (1968). Hiernaux records that he used samples that contained at least 40 individuals, and only adult males were included. Female African data are taken from Eveleth and Tanner (1976: Appendix Table 45).

## Asia

"Asian" (or Mongoloid) is a very loose term for a group that inhabits, or formerly inhabited, perhaps two-thirds or more the world's land-surface. Although they share physiognomical characteristics that may have a relatively recent origin (Brown 1992a), they are a varied group, and have been broken up into regional samples covering Southeast Asia, East Asia, North Asia on the one hand and the Americas on the other. Although the majority of these data were taken from Eveleth and Tanner (1976 Appendix Tables 61 and 62), several other sources were also used including Birdsell (1941), Ai *et al.* (1993) and Dai *et al.* (1966).

## Oceania

Populations in this group include those commonly designated as Melanesian and Polynesian. The evidence from linguistics, archaeology and biology indicate that Oceania has a complex ethnic history and that in some cases a sharp delineation between Melanesians and Polynesians, at least in Near Oceania (that part of Oceania closer to the landmasses of the western Pacific), are artificial and somewhat arbitrary (Houghton 1996). While it is easy enough to categorise PNG Highlanders as Melanesian and the people of Remote Oceania as Polynesian there are many groups that defy any categorisation on the basis of phenotype (Houghton 1996; Howells 1973a) and the region is one of extreme diversity.

The majority of these samples come from Eveleth and Tanner (1976, appendix Tables 93 and 94) with some other groups coming from Houghton (1996) and Littlewood (1972).



Compared to other areas of the world the anthropometric data for this region are not extensive.

### **Indo-Mediterranean**

This is a diverse region that covers Southwest and South Asia and the Mediterranean coast of Africa. These samples come from Eveleth and Tanner (1976, appendix Tables 77 and 78) and Edholm (1966).

## **4.3.2 Osteometry**

### **4.3.2.1 Introduction**

A limited number of variables were studied in an osteometric sample. These measurements consisted entirely of limb segment lengths. Limited data were available from anthropometric surveys for these measurements and the use of osteometric data were necessary to assess the ecogeographic correlations of limb segment lengths ratios in a world sample.

### **4.3.2.2 Australia**

#### **Murray Valley**

This is a large series collected by G.M. Black between 1937 and 1950 in the Murray Valley region on the borders of New South Wales and Victoria (Brown 1989: 7 - 8). The sample consists of 47 adult male and 53 adult female crania and assorted postcrania and were collected in the period 1943 to 1950 in an area between Chowilla and Coobool in the Murray Valley (Brown 1981a; Sunderland & Ray 1959). This collection is undated and there is, in fact, no precise information regarding the location of the finds, or their stratigraphic and archaeological contexts. However, a morphological and metrical comparison of these crania with Kow Swamp, Barham and Roonka conducted by Brown (1989), and the multivariate analysis of Pietruszewsky (1979) suggests that they are a relatively recent population. The collection was reburied in 1985 and all measurements used below were taken by Peter Brown (1989). Only the male postcrania were included in the subsequent analysis (Chapter 9).

### **4.3.2.3 World**

#### **Asia: Recent Southern Chinese**

This is a modern southern Chinese sample of known age and sex. The sample consists of 38 adult males of known age and sex that were part of the Peking Medical College

Collection of Davidson Black. These data were collected by Peter Brown (2000a).

### **Other**

Postcranial measurements from a selection of recent human populations have been taken from Trinkaus (1981: 202, Table 5). These populations include Lapps (Norway), Eskimos (Alaska), Europeans (Yugoslavia), Euro-Africans, Euro-Americans, Native Americans (New Mexico), Native Americans (Arizona), African (Bantu), African (San), African (Pygmies), African (Egyptians), African Americans, and Melanesians (New Calendonia). Only the values for the male postcrania were used. The sample sizes and sources for this data can be found in Trinkaus (1981: 202-204).