

GENETIC ASPECTS OF GROWTH AND OF POPULATION
STRUCTURE IN INDIGENOUS PEOPLES OF AUSTRALIA
AND NEW GUINEA

by

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ABSTRACT

Studies of two distinct research areas within the framework of Human Population Genetics are presented. Part I examines the extent to which genes may be responsible for the control of quantitative characteristics. Weight, height and head circumference as a function of age for full-blood and part-blood Australian Aborigines from the Northern Territory, Queensland and Western Australia are compared. Part-bloods tend to be heavier than full-bloods at birth, and further division of the children into groups according to whether their parents are full-blood or part-blood suggests that the genes inherited from the mother and in the case of males the Y-chromosome inherited from the father, have a distinct effect on birthweight. These results are supported by the intraclass correlation coefficients for birthweight of sib-pairs and cousin-pairs.

The technique of regression is used to compare mean growth curves of Aboriginal children with those of white children. For males white children are bigger than part-bloods who are bigger than full-bloods. Female full-bloods and part-bloods tend to cluster together while female white children are significantly bigger. Comparison of growth measurements for individual Aboriginal children with accepted standards shows that weight is most likely to be below standard. Time series analysis of individual growth curves is used to obtain sib-pair and cousin-pair intraclass correlation coefficients; the results suggest that after birth environmental factors dominate growth of Aboriginal children, although genetic effects especially in the case of females are still significant.

Part II of this study deals with the extent of genetic differentiation among the indigenous peoples of Australia and

New Guinea. The technique of kinship calculated from gene frequencies of blood genetic markers is used to examine population structure. The results of this analysis are in general agreement with results from linguistic studies; however, the genetic technique appears to have greater "resolution". The decrease in genetic relationship with geographic distance occurs at a much faster rate in New Guinea than in Australia, and is probably a function of the ease of travel within the areas studied.

Genetic similarities between some Melanesian peoples and northern Australian Aboriginals determined from this study contrasted with the lack of linguistic similarities between these populations suggest that the Australians tended to be unaffected culturally by contact with outside populations. It is suggested that the combination of genetic and linguistic studies of relationships among populations can be used to infer the extent of contact between the study groups.

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Chapter 1

INTRODUCTION

Human Population Genetics

Human Population Genetics is concerned with the inherited differences which are found among individuals. These differences may be quantitative or qualitative, but they are all determined to some extent by genes which are transmitted from one generation to the next according to the principles of Mendelian genetics. The theoretical basis of population genetics was established by Fisher (1918), Wright (1921) and Haldane (1932), in their formulations of the mathematical theory of evolution. These works attempt to provide an understanding of the nature and source of the genetic variability found in human populations.

Genetic variation can be seen by examining either quantitative or qualitative characteristics of populations. The phenotype may be modified by non-genetic factors. In the case of variation for quantitative characteristics, therefore, analysis must attempt to assess both the environmental and genetic contributions. Since qualitative characteristics, on the other hand, vary in a discrete manner, individuals may be divided into distinct types despite variation in the environment. To the extent that this discrete variation can be assigned to genes at specified loci it can be used as a measure of genetic differentiation among populations.

A complete understanding of the genetics of human populations would require information on the range of variation in both quantitative and qualitative traits, with a specification of the impact on these of environmental variables. The ideal is difficult to achieve, but human populations in Australia and New

Guinea offer unique opportunities for approximations to such studies because of the range of environments and the relative isolation of the numerous populations. This relative isolation has been maintained until recently under conditions similar to those which must have existed during the greater part of the evolution of modern man. In addition recent changes resulting from contact with alien but dominant cultures has led to alterations in the environment and also to hybridization between persons from widely different gene pools, making possible another approach to the study of gene-environment interactions.

The People

The presence of man in Australia and New Guinea is now known to have a considerable time-depth. Man is thought to have reached New Guinea and northern Australia at least 50,000 years ago (Hope and Hope, 1976) and recent evidence suggests he had reached southern Australia by 40,000 B.P. (Bowler, 1976). For the greater part of this period, Australia and New Guinea formed a single land mass and it was not until approximately 8,000 B.P. that rising sea levels at the end of the Pleistocene separated the two countries by creation of the Torres Strait (Jennings, 1972).

The present indigenous inhabitants of Australia and New Guinea are physically and culturally distinct from one another, and they are not homogeneous even within the boundaries of the two countries. The people who first lived in Australia and New Guinea were hunter-gatherers who moved around in small groups. Gajdusek (1964) pointed out that small primitive groups of this type would have been critically affected by events such as floods, droughts and famines; these natural disasters together with social disruption brought about by warfare,

splitting and merging of groups and changes in mating patterns would have had great impact on their genetic structure. In addition, new genes were probably introduced by later migrations to the two countries from outside the area.

When European settlers arrived in Australia (c. 200 B.P.) the Aborigines were still hunter-gatherers, each small organized group being called a band. Marriage and trade took place between bands within regions, and Peterson (1976) has suggested that these regional clusters may have been determined by natural factors such as drainage basins, rather than by the tribal groupings discussed by Birdsell (1973). The significance of the river systems in determining trade routes has been pointed out by McCarthy (1939) who also noted that the formation of intergroup friendships and marriages were an important part of the gatherings arranged for barter, a fact which suggests that in some areas, though not in all, marriages between people belonging to different language groups may not have been uncommon. Today most of the full-blood Aborigines live in settlements often with members of several different linguistic groups in each community. During the last three or four generations, therefore, the number of inter-group marriages has probably increased, particularly between groups where previously they had been rare.

The people of New Guinea, particularly those in the highlands began to practise agriculture well before Europeans arrived in their country (Howells, 1973). Two major ecological zones were occupied, one in the highlands and the other on the coastal plains. The people of the highlands frequently were isolated from each other and from the coastal peoples, because of the difficulty of travel in the highlands and because of the

sharp changes in temperature which occur with altitude (Brookfield, 1964). Even coastal populations in many areas were isolated from neighbouring groups by swampy terrain, with communication in many instances being possible only along river systems.

The basic unit (local group) in New Guinea traditionally was either the village or the hamlet group, and usually consisted of members of several clans. Sometimes members of the same clan belonged to different local groups, and marriages always took place between groups (Langness, 1964). Warfare was a major characteristic of the indigenous people of New Guinea, particularly in the highlands. In some areas members of the winning side chose wives from the defeated side (Berndt, 1964). There is also evidence of marriages taking place between members of different linguistic groups and recent studies have shown the percentage of marriage migration to be quite high in some parts of the country (Malcolm *et al.*, 1971). Since the arrival of Europeans in New Guinea, roads have been built to enhance movement between the highlands and the coast. This increase in mobility has probably led to an increase in marriage migration during the past forty years.

Outline of Thesis

This study of quantitative and qualitative characteristics of the indigenous populations of Australia and New Guinea is divided into two parts.

PART I (consisting of Chapters 2 to 5) uses data on the growth of Australian Aboriginal children to infer the importance of genes in determining these quantitative characteristics. The measurements consist of weights, heights and head circumferences of children from the Northern Territory,

Queensland and Western Australia. (During the course of this project it was not possible to collect comparable data on the growth of children in New Guinea). Mean growth curves for Aboriginal children living in different parts of Australia are determined over the age range from birth to four years. Some of these curves are shown to differ significantly from one group to another and from growth curves of white Australian children. Correlations among the variables are found to be higher for part-blood children than for full-blood children. Weights at different ages tend to be more highly correlated than heights and head circumferences. Analysis of the mean birthweights of full-bloods and part-bloods suggests that the genes inherited from the mother (and in the case of males, the Y-chromosome inherited from the father) play an important part in determining increase in weight before birth. Calculations of the intraclass correlation coefficients for sib-pairs and cousin-pairs support these results. Methods of time series analysis are used to study the individual growth patterns of the children, which allows each growth curve to be represented by a parameter value. The sib-pair and cousin-pair intraclass correlations obtained for these parameters suggest that after birth environmental factors play a dominant role in determining growth of Aboriginal children, although genetic effects are still resolved. Female growth seems to be under closer genetic control than that of males.

In PART II (consisting of Chapters 6 to 10) qualitative characteristics detectable in blood are used to analyse the genetic structure of indigenous populations of Australia and New Guinea. The variation in these genetic markers (blood group antigens, red cell enzymes and serum proteins) is analysed in order to demonstrate genetic differences between

populations in Australia and New Guinea. Genetic distance measures are calculated between pairs of populations from the gene frequencies of the markers within these populations. The results are compared with inferences from linguistic studies in this region. The analysis shows that there is a great deal of genetic diversity among populations of Australia and New Guinea, which is generally in agreement with results from linguistic studies, although the genetic marker technique seems to have greater "resolution". Further, the genetic analysis indicates that there has been gene flow between Melanesia and Australia in the past.

PART I

GENETIC STUDIES OF GROWTH IN AUSTRALIAN
ABORIGINAL CHILDREN

Chapter 2

REVIEW OF GROWTH STUDIES

Growth Measurements of Australian Aboriginal Children

Previous studies show that in many cases the growth pattern of Australian Aboriginal children differs from that of white children. Jose and Welch (1970) divided the process of growth in Aboriginal children into four periods: 1) early normal growth (birth to six months); 2) complete or partial cessation of growth (six months to two years); 3) slow catch-up (two to six years); 4) rapid catch-up (seven to eleven years). The data for their study were collected from settlements and missions in Queensland, but growth of Aboriginal children in other parts of Australia shows similar trends. Kirke (1969) measured heights and weights of full-blood central Australian Aboriginal children under five years of age. He found that the percentile distribution of these parameters for the age group under six months was about the same as for white children. From six to eleven months there was greater representation in the lower percentiles, and this pattern continued and became most severe in the group aged 18-23 months where 41.5% for height and 25.5% for weight were below the third percentile of the British standards reported by Tanner *et al.* (1966). After two years there appeared to be an improvement, but Kirke (1969) suggested that this might be due to very high mortality among infants in the low percentiles for weight. Using longitudinal height and weight records of full-blood children from birth to five years at three Arnhem Land Missions, Kettle (1966) calculated standard growth curves for Aboriginal children. She found that Aboriginal children grew more rapidly than white

Australians for the first six months after birth, but by twelve months of age they were about 1.8 kg lighter and this difference increased with age. Height showed a similar pattern although the difference was less marked. Each of these studies is supported by others which show an over-representation in the low percentiles, and an interruption of growth between the sixth and twelfth months (Elliott *et al.*, 1967; Copeman *et al.*, 1975; Parsons, 1965; Propert *et al.*, 1968; Clements and Jacobs, 1968; Maxwell and Elliott, 1969; Jose *et al.*, 1969).

Although Aboriginal growth during the first six months of life is considered to be similar to that of white children, their birthweights are generally lower. At Yuendumu in central Australia Brown and Barrett (1972) obtained average birth weights of 3.1 kg for boys and 2.9 kg for girls. These are 0.4 kg and 0.5 kg below the British averages for boys and girls, respectively, reported by Tanner *et al.* (1966). Kettle (1966) calculated mean birthweights of 2.9 kg for both boys and girls in Arnhem Land, and mean birth-lengths of 49.8 cm for boys and 49.5 cm for girls. Parsons' (1965) data from central Australia gave mean birthweights of 3.1 kg for males and 3.0 kg for females. A study by Propert *et al.* (1968) covering Mornington Island, central Australia and localities in Western Australia, gave mean birthweights of 3.3 kg for males and 3.1 kg for females at Mornington Island, 3.1 kg for males and 3.0 kg for females in central Australia and 3.0 kg for both males and females in Western Australia. In addition they obtained some part-blood data from Western Australia, and mean birthweights were found to be 3.3 kg and 3.2 kg for males and females, respectively. A survey in which most of the children were part-bloods was carried out by Edwards (1970) in Walgett

(New South Wales), and the mean birthweight was found to be 3.0 kg. At Cherbourg in Queensland, Stuart *et al.* (1972) found that 7% of children had birthweights below 2.5 kg, while in central Australia, Maxwell and Elliott (1969) found the percentage to be 12.5. Growth retardation was found to be not as severe among part-Aboriginals in Sydney as among Aboriginals elsewhere (Lickiss, 1970).

Although growth measurements for age do tend to be lower for Aboriginal children than for white children, they are by no means small in relation to world averages. For example, the values obtained by Malcolm (1970) for Bundi children in New Guinea are lower than those for Aboriginals. Meredith (1968) summarized weights and heights of contemporary groups of pre-school children, and found that for four year olds, the mean body weight ranged from 11.1 kg to 17.3 kg, and mean height from 85.8 cm to 103 cm. For Aboriginal children of this age, Kettle (1966) obtained mean weights of 14.1 kg for boys and 13.7 kg for girls, and mean heights of 98.1 cm for boys and 97.8 cm for girls.

Jose and Welch (1970) concluded that although genetic factors may influence growth, malnutrition affecting a broad range of nutrients is an important cause of growth retardation. In support of this conclusion, they found normal growth patterns at two missions where particular attention was given to early supplementary infant feeding. Moodie (1973) attributed the decline in growth rate of Aboriginal children to a partial failure of the quality and quantity of the mother's milk, and to the onset of a period of repeated respiratory and gastrointestinal infections. Elliott and Kneebone (1968) found that the lactose content of Aboriginal

breast milk decreased markedly after the sixth month of lactation and that breast milk production did not increase with the age of the infant. They suggested that these two factors probably contributed significantly to fall off in growth rate after six months of age. In Queensland, Jose *et al.* (1970) found that retardation of growth in infancy was related to an elevated erythrocyte sedimentation rate as well as high incidence of infection and high antibody levels. In 1970, Edwards set out four factors which he considered led to malnutrition and growth retardation:

- 1) Poor socioeconomic background;
- 2) Apathy and ignorance of the mother, which is reflected in poor attendance for antenatal care;
- 3) Failure of breast feeding;
- 4) "Vicious circle effect". When breast feeding ceases, malnutrition commences, leading to diarrhoea and failure to absorb food, as well as increased susceptibility to infections. This leads to a worse state of malnutrition and so a recurring pattern is set up.

According to Jose and Welch (1970) growth retarded Aboriginal children are more anaemic and their blood concentrations of various nutritional factors are lower than those of normal Aboriginal children. They also suggested that high infection rates helped to maintain the retardation of growth of these children. Best *et al.* (1976), however, found that treatment of young children infected with intestinal parasites did not produce a growth spurt and that despite multiple infections they maintained a satisfactory growth rate. This has also been reported by Dawson (1963) in Sierra Leone and by McGregor *et al.* (1956) for Gambian children. Similarly, Tanner (1966) found that eradication of malaria and other parasitic infections in

Africa and South America did not produce notable effects on the growth of the children.

Measures of Nutritional Status and their Application to Australian Aboriginal Communities

Several people have discussed ways of using retardation of growth as a measure of degree of malnutrition. Jelliffe (1966) claimed that weight is the key anthropometric measurement in indicating malnutrition with the degree of malnutrition being classified according to percentage levels below the standard weight. The first classification was that of Gomez *et al.* (1955) who selected three levels (90%, 75% and 60%). Jelliffe (1966) considered that for simplicity, the levels should be 90%, 80%, 70%, 60% below standard. Copeman *et al.* (1975) used Jelliffe's (1966) classification to assess the growth of Aboriginal children living in and around Cunnamulla in western Queensland. Applying Jelliffe's (1966) standards, they found that 46% of the children were suffering from mild to moderate protein-calorie malnutrition. Ford (1964) has suggested that 66% of the standard weight should be regarded as the "malnutrition line", because the rate of basal metabolism alters after the loss of one-third of body weight. Maxwell and Elliott (1969) agreed with Ford (1964) that comparison of measurements with standard values is of great value in assessing malnutrition. They examined pure-blood Aborigines living in central Australia to look for nutritional effects, and found that no age group had normal percentile distributions by white standards. Birth to six months was the least affected age group with about 30% below the tenth percentile for weight and height. The most marked abnormality occurred between the first and third birthdays for weight and first and fourth birthdays for height with more than 80% falling

below the tenth percentile. Head circumference showed a similar trend with approximately six percent falling below the tenth percentile between birth and six months and more than 40% falling below the tenth percentile from seven months to three years. They concluded that most of the children were malnourished during their first year of life, and that in many cases the effect of malnutrition remained for the rest of their lives.

The index of growth retardation defined by Jose and Welch (1970) provides another measure of nutritional status. It is based on the standard growth charts of Tanner *et al.* (1966) and may be written as

$$\text{Growth Index(\%)} = \frac{\text{weight(height) age at 50}^{\text{th}} \text{ percentile}}{\text{chronological age}} \times 100$$

where weight (height) age at 50th percentile = age for which the child's weight (height) corresponds to the 50th percentile curve of the standard growth charts.

Jose and Welch (1970) define a growth retarded child as one having a height and weight index of less than 70%, and a normal child as one for whom both indices are greater than 90%. In their examination of six Aboriginal Settlements in Queensland they found half of the children were growth retarded and 16% had a growth index of 50% or less.

Other classifications of malnutrition based on weight and height measurements have been suggested. For example, Seoane and Latham (1971) and Waterlow (1972,1974) considered that weight for height is an index of current nutritional status, while height for age measures retardation and therefore past malnutrition. Criticism of these measures has come from Maaser and Droese (1971) who surveyed overnutrition and over-weight in West German children, and commented that nutritional status

cannot be assessed from height and weight measurements alone. Also Garn (1965) has questioned the practice of using standards of one race for another, but Habicht *et al.* (1974) claim that there is no evidence for ethnic differences in growth potential during the early years of life, and therefore it is justifiable to apply the norms of developed countries to other communities. It is unlikely that nutritional status of a community can be assessed simply from growth measurements. However, measures of growth retardation such as those of Jelliffe (1966) and Jose and Welch (1970) provide a useful method for classifying the growth of children.

Relationship between Nutrition and Growth

Several studies indicate that the nutrition of Aboriginal infants and children does not reach the standard set by white populations (Kirke, 1969; Walker and Harry, 1972; Gracey, 1973). Hitchcock and Gracey (1975) found that the nutrition of children was low in calories and vitamin C in a rural Aboriginal community in south-west Australia. However, as Durnin *et al.* (1973) point out, the energy requirements of man and his balance of intake and expenditure are not known. This seems to be the appropriate conclusion from studies of subjects with similar attributes and activities whose calorie intakes vary widely (Rose and Williams, 1961). Widdowson (1962) found that from the age of one year (and probably earlier), large differences in calorie intake are evident from one individual to another, but they do not necessarily correspond with differences in body weight. Her analysis showed that variation in losses through the bowel (that is, differences in amount digested) is negligible for calories, but is important for calcium and other minerals. Some people are good absorbers of

calcium and others are bad, and this individuality is present soon after birth. She concluded that many nutritional characteristics are inherited.

Several studies have indicated that the level of activity of an individual as well as the level of nutrition, affects growth. Mack and Kleinhenz (1974) examined infants during the first eight weeks of life and noted that patterns of activity, calorie intake and weight gain appear to commence with the earliest days of life. Sontag (1965) found that intrauterine activity differs significantly from one child to another, which suggests that growth may be controlled by activity even before birth. In an examination of infants aged from four to six months, Rose and Mayer (1968) found that calorie intake was more closely related to degree of activity than to body size, and that it was not related to growth. Mayer and Thomas (1967) believe that energy balance is a major factor in determining body fatness and frequency of eating. They proposed that there is a complex regulatory system which controls food intake such that energy intake is closely matched to energy expenditure despite marked variations in the energy requirements of the organism and the nutrition value of the diet. That is, energy balance is normally maintained by a precise and reliable physiologic mechanism, and the energy surplus represented by obesity may reflect direct failure of this mechanism, or some combination from a variety of neurological, endocrine, enzymatic and psychological disorders. Energy intake, activity and growth, therefore, may be largely under genetic control.

Growth is the result of cell multiplication and enlargement. Body fat cells appear in the fetus late in gestation, with the period of most rapid growth, as judged by increase in skinfold

thickness, coming during the first nine to twelve months after birth (Tanner and Whitehouse, 1962). Cheek *et al.* (1970) stated that overfeeding in early life can lead to elevation of growth hormone and insulin, an overgrowth of the lean body tissue and a forcing of skeletal growth. This results in an accelerated bone age, increased skeletal height, and early achievement of puberty. Brook (1972,1973) claimed that there is an increase in adipose cells among children who become obese during the first year of life, relative to children of normal weight and children who become obese after the first year of life. Thus it appears that overfeeding in early life may have serious life-long sequellae in the form of excess adipose cells. This hypothesis is supported by Winick and Noble (1967) who found that reducing the litter size of rats produced persistent excess growth. The rats were found to have normal sized cells but an increased number of fat cells, which is in accord with the findings of Zingg *et al.* (1962). A decreased fat cell count was found if the litter size was increased (Winick and Noble, 1966). Early malnutrition caused by the increased litter size resulted in permanent stunting, while later malnutrition did not. Winick and Noble (1966) felt that this difference could be explained by differential effects on cell size and cell division, and that the same explanation might apply to children. These results are supported by Widdowson (1970) who found that in mammals, the size that an undernourished animal can be expected to attain after rehabilitation depends on the stage of development which has been reached at the time of undernourishment. If undernourishment occurs when differentiation and division is taking place most rapidly, complete rehabilitation may never occur.

However, if the complete cell number is present, rehabilitation is achieved quite readily. According to Winick and Rosso (1969) the earlier the nutritional stress takes place, the more severe will be its effects. Chase and Martin (1970) compared nineteen children who had been hospitalized for undernutrition during the first year of their life with a control group, three to four years later. The test group was found to be lower in height, weight and head circumference. Those who were treated before four months of age, however, were not as far below the control group as those who remained undernourished after four months of age.

It is clear that increments in cell size and cell number are a function of time, and that genetic influences, the action of hormones and the nutritional status during development are involved. The question of why certain genes become active at different times could provide the answer to how growth is controlled. For example, a number of enzymes not found in fetal liver appear in the newborn, indicating that there may be a definite genetically controlled response to birth (Cheek *et al.*, 1970).

Genetic Control of Growth

In 1974, Mack and Ipsen showed that by four months of age, a weight to length pattern has emerged which carries significant power for the prediction of the weight to height relationship at twelve and 48 months. These data suggest that the first few months of life are critical in establishing long-lasting patterns of body configuration. Further, Tanner (1962) has shown that a very strong correlation exists between the body length achieved in the early months of life and height in adulthood among people who were exposed to an adequate

nutritional environment as infants. At two months the correlation is about 0.5 and the value increases to 0.6-0.7 by the latter part of the first year of life. This correlation, however, is not as strong for weight. It appears that with adequate nutrition, an infant's linear growth velocity is predominantly under genetic control.

Studies concerned with the genetic control of growth parameters have generally dealt with the degree of quantitative resemblance between genetically related individuals. Birth-weight data has been analysed many times to determine the relative roles of genotype and environment. In 1939, Donald obtained an average sib-pair correlation for birthweight of 0.54, while a later study by Karn *et al.* (1951) found a correlation of 0.43. Morton (1955) has carried out an informative investigation of the genetics of human birthweight. He collected birthweights of children born in Hiroshima and Nagasaki from 1948 to 1952, and analysed the data as paired observations of sibling relationships. The intraclass correlation coefficient for maternal half-sibs (0.58) was slightly higher than that of like-sexed twins (0.56) and adjacent full-sibs (0.52). The correlation value for unlike-sexed twins (0.66) was greater than that for like-sexed twins, while adjacent sibs were more alike than those between whom there were intervening births. Morton (1955) concluded from these results that the resemblance in birthweights of sibs is largely attributable to the maternal environment and not to the genetic similarity of sibs. Robson (1955) obtained data on cousin pairs born in London, and after adjusting the birthweights for sex and parity, she obtained product-moment correlations of 0.14 for children of sisters, 0.02 for children

of brothers and 0.01 for children of a brother and sister. These results imply that the maternal genotype plays an important part in the determination of birthweight. Using data on twin and single births, Penrose (1961) partitioned the causes of birthweight variation in a stable Western European community and attributed 38% to hereditary factors.

Other quantitative characteristics have been studied to examine the way in which they are influenced by genetic and environmental factors. Howells (1966) calculated intraclass sibling correlations for thirty measurements taken on people between the ages of 15 and 59 years belonging to a religious sect distributed in colonies in the western United States and Canada. The values range from 0.17 for ear length and 0.18 for ear breadth to 0.47 for stature and 0.48 for nose height. McHenry and Giles (1971) obtained values ranging from 0.06 for head breadth to 0.45 for iliospinale height for the inhabitants of three adjacent villages in the Markham Valley of New Guinea.

It is commonly observed that tall parents tend to have children who are tall for their age (Tanner, 1962). This suggests a genetic control of growth, although environmental influences obviously play a part. Malcolm (1970) has compared parent-offspring height and weight correlations for European children with those for Bundi and Kaiapit children in New Guinea. The values for European and Kaiapit children were high and mostly significant, but the Bundi children had low values suggesting that adverse environmental conditions had affected their growth. A study by Bieliński and Welon (1966) of Polish children showed that height correlations with the midparent were higher than those with either parent taken separately; father-child and mother-child correlations were

roughly equal; daughters tended to be more highly correlated with their parents than were sons. As there had been marked environmental changes during the last generation, they speculated that this between-sex differential could be attributed to the better canalization of growth in the female than in the male. That is, it may be a reflection of the fact that girls are less easily thrown off their genetically determined growth curves by environmental stresses than are boys.

Curve-Fitting and Longitudinal Data Analysis

Longitudinal data allow individual growth curves to be examined. In order to analyse these data, functions are generally fitted to them; the most frequently used are the exponential, logistic and Gompertz curves. Malcolm (1970) fitted the regression equation, $y = \alpha + \beta t + \gamma \log(t)$ first proposed by Jenss and Bayley (1937), to cross-sectional heights and weights of Bundi children from birth to 12 years of age. He found that both α (initial status) and γ (rate of deceleration of growth) were greater in females than in males. He also fitted this equation to data from two major clans and found that β (rate of growth) was significantly greater for the Chimbu than for the Non-Chimbu, and suggested that this was due to genetic variation in growth rate. Vandenburg and Falkner (1965) fitted a similar equation, $y = \alpha + \beta t + \gamma t^2$ to longitudinal height data of monozygotic and dizygotic twins from birth to four years of age. They found that hereditary factors were significant for β and γ but not for α .

The period of growth from birth to two years has been studied by Wingerd (1970). His method, based upon a paper by Rao (1958), does not require the a priori choice of a mathematical function. Instead, the time scale is transformed

in a fashion which forces the mean curve into a straight line, from which the distance, velocity and acceleration relative to the group means can be obtained for each child. Bialik *et al.* (1973) have also examined the first two years of post-natal growth. They chose five functions and fitted them to individual weight data for infants in Israel by least squares. The analysis showed that the equation, $\ln(W) = \alpha + \beta \ln(t) + \gamma \ln^2(t)$, could accurately fit weight growth in infancy. Grouping the children according to birthweight showed that those with a birthweight below 2.5 kg grew more rapidly than those with a higher birthweight, while those with a birthweight above 4.0 kg grew more slowly than other children.

The Jenss-Bayley curve was used by Manwani and Agarwal (1973) to examine the change in height, weight and head circumference of Indian children during their first year of life. The curve fitted well for height and head circumference, but it did not fit the weight measurements of some of the children; this seemed to be due to short illnesses that they had suffered. This study demonstrated that the velocity of head growth in infancy decelerates faster than that of height and weight.

Techniques for the analysis of longitudinal data sets are reviewed by Kowalski and Guire (1974). They suggest that an important consideration in the study of growth should be the correlations among successive observations, which may be measured using the autocorrelation function for different lags. Hirschfield (1970a, 1970b) applied these methods of time series analysis to human craniofacial growth data and concluded that the time series approach has greater applicability, and can yield more accurate predictions of growth than regression methods.

The statistical techniques and computer programs used in the present analysis of Australian Aboriginal growth are discussed in Appendix 4.

Chapter 3

WEIGHTS, LENGTHS AND HEAD CIRCUMFERENCES OF AUSTRALIAN
ABORIGINAL CHILDREN

The majority of full-blood Aboriginals live in Government Settlements and Church Missions in northern Australia. These communities range in population size from under 200 to over 1,000, and some of the services associated with European society are provided. The people rely primarily on the stores for their food, although some of the communities provide supplementary feeding centres for infants and young children.

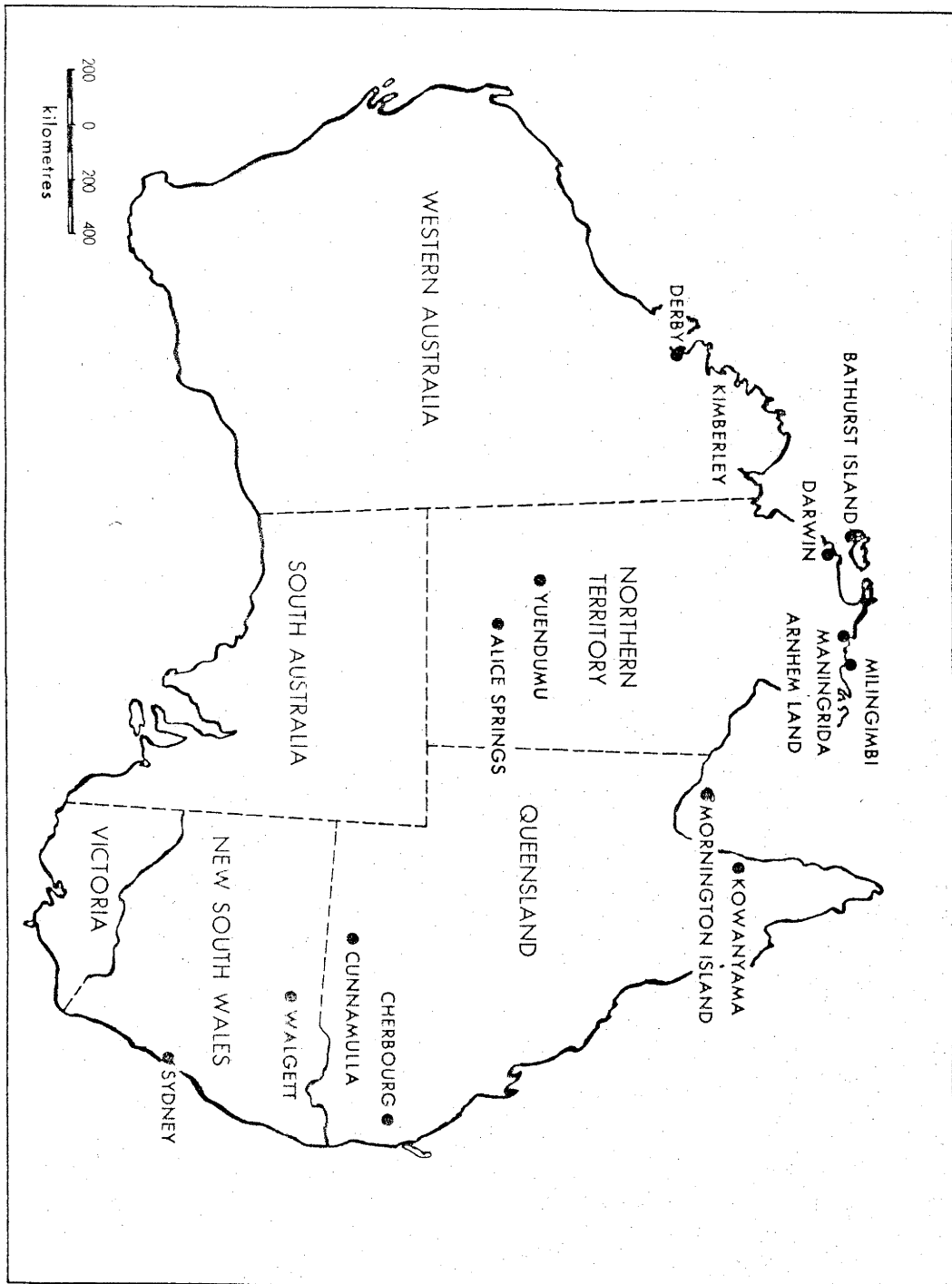
The Sample Populations

For this study, data were collected from three communities in the Northern Territory and Queensland, and from the Kimberley region in Western Australia (Map 1). In the Northern Territory, Maningrida, a Government Settlement, has a population of about 1,000, while Bathurst Island, a Catholic Mission, and Milingimbi, a Methodist Mission, have populations of between 800 and 900. The majority of the Queensland data were collected from Kowanyama, a Government Settlement with about 700 Aboriginals in Cape York, although additional information was obtained from two other Settlements in the State. The data from the Kimberley were from a large number of Aboriginal communities scattered throughout the northern region of Western Australia.

The quantity of data varied from place to place. The Northern Territory data were obtained from Dr D.S. Jacobs of the Department of Health in Darwin and consist of a mixed longitudinal series of measurements for weight, height and

MAP 1

Map of Australia showing the places where growth studies
of Aboriginal children have been done



head circumference covering the age range birth to four years for 102 males and 79 females from Maningrida, 39 males and 46 females from Bathurst Island, and 19 males and 20 females from Mililingimbi. All of these children are full-blood Aboriginals. Similar records were obtained from the hospital at Kowanyama (Queensland) where the children are measured regularly by the nursing sisters. These measurements are for 35 full-blood and 23 part-blood males and 30 full-blood and 16 part-blood females. In addition birthweight data were provided by Dr I.A. Musgrave, of the Queensland Department of Health, for children living on two other Settlements in Queensland. This sample consists of 25 full-blood and 36 part-blood males and 16 full-blood and 39 part-blood females. Birthweights for 156 full-blood and 101 part-blood males and 123 full-blood and 102 part-blood females from Western Australia were made available by Dr R.M. Spargo, the Regional Medical Officer for the Kimberley Division of Community Health Services in Derby, Western Australia. All of the children included in this study were born between 1960 and 1972; emphasis was placed on obtaining measurements for sets of sibs.

Mean Birthweights

The birthweight data were divided into 18 subsets based on sex and whether the individuals were full or part-bloods. Results from the STATJOB analysis program UNISTAT1 (see Appendix 4) suggest that birthweight is normally distributed in each subset of the data. Sample sizes, means, standard deviations, and percentile distributions for all subsets are given in Table 1. The Student's t-test (see Appendix 4) was used to compare the means, and showed that the mean birthweights for males and females are significantly different at Maningrida

TABLE 1

Means, Standard Deviations and Percentiles								
for Birthweight (kg)								
<u>Males</u>	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
Full-blood								
Maningrida	100	2.878	.51	1.7	2.6	3.0	3.2	3.6
Bathurst Is.	39	2.752	.36	2.3	2.5	2.6	3.0	3.5
Milingimbi	19	3.069	.30	2.4	2.9	3.1	3.2	3.6
Kowanyama	35	3.017	.49	2.3	2.6	3.1	3.3	4.1
Queensland	60	3.003	.54	2.2	2.7	3.0	3.3	4.0
Kimberley	156	3.082	.51	2.1	2.8	3.0	3.4	4.0
Part-blood								
Kowanyama	23	3.022	.59	2.1	2.6	3.0	3.4	4.1
Queensland	59	3.236	.50	2.4	2.9	3.3	3.6	4.1
Kimberley	101	3.300	.49	2.6	3.0	3.3	3.7	4.1
<u>Females</u>								
Full-blood								
Maningrida	79	2.680	.39	2.0	2.5	2.7	3.0	3.3
Bathurst Is.	46	2.679	.54	1.8	2.3	2.6	3.1	3.6
Milingimbi	20	2.693	.48	1.7	2.2	2.8	2.9	3.3
Kowanyama	30	2.874	.36	2.3	2.7	2.9	3.1	3.4
Queensland	46	2.879	.46	2.0	2.7	2.9	3.2	3.7
Kimberley	123	3.009	.50	2.2	2.7	3.0	3.3	3.8
Part-blood								
Kowanyama	16	2.850	.49	1.9	2.4	2.9	3.2	3.6
Queensland	55	3.136	.64	2.3	2.7	3.1	3.6	4.2
Kimberley	102	3.122	.46	2.4	2.8	3.1	3.4	3.9

($pr < .01$; where the number shown indicates that the probability that the means are the same is less than .01), Milingimbi ($pr < .01$) and for part-bloods in the Kimberley ($pr < .01$), although in all cases the mean birthweight for males is higher than that for females. In the Queensland and Kimberley samples, part-bloods were found to be significantly heavier than full-bloods for Queensland males ($pr < .02$), Queensland females ($pr < .05$) and Kimberley males ($pr < .01$). No significant difference* was found for Kimberley females. The mean birthweight of part-blood males at Kowanyama is greater than that of full-blood males, but the mean birthweight for part-blood females is smaller than that for full-blood females; however, neither of these differences are significant.

Analysis of the significance of differences in mean birthweight among populations showed that full-blood males at Bathurst Island are significantly lighter than those at Milingimbi ($pr < .01$), Kowanyama ($pr < .02$) and Queensland ($pr < .02$) and both Bathurst Island and Maningrida full-blood males are significantly lighter than those from the Kimberley ($pr < .01$ for both). For full-blood females, those from Maningrida are significantly lighter than those from Kowanyama ($pr < .05$) and Queensland ($pr < .05$). The Maningrida, Bathurst Island and Milingimbi females are all significantly lighter than the full-blood females from the Kimberley ($pr < .01, < .01, < .02$, respectively). Kowanyama part-blood males are significantly lighter than those in the Kimberley ($pr < .05$), and the same is true for females ($pr < .05$). In all categories there are no significant differences between Kimberley and Queensland children.

For the Queensland children, information was available as

* Throughout this thesis not significant means $pr \geq .05$.

to whether their parents were full-blood or part-blood. The data for these children were separated into four groups according to the blood types of their parents (both full-blood, one parent part-blood, both part-blood), and the mean, standard deviation and percentiles of birthweight were calculated for each group (Table 2). None of the sex differences are significant. However, when both parents are full-blood Aborigines, female children are significantly lighter at birth than when both parents are part-blood ($p < .02$) or the mother alone is part-blood ($p < .05$). If only the mother is full-blood the female children are again lighter than when both parents are part-blood or the mother alone is part-blood, but these differences in mean birthweight are not significant. In the case of males, the mean birthweight for full-bloods is less (but not significantly) than that for those for whom either or both of their parents are part-bloods. Therefore, it appears that for females, birthweight depends primarily on the mother's genes whereas for males the father's genes seem to play a part in determining birthweight. This is seen again when the children are grouped according to (i) the blood type of their mother (full or part) (ii) the blood type of their father (full or part) (Table 2). For males, the mean birthweight is lower (though not significantly) for those whose mother is full-blood than for those whose mother is part-blood. Similarly males with a full-blood father are lighter at birth than those with a part-blood father. For females, however, the children with full-blood mothers have a significantly lower mean birthweight than those with part-blood mothers ($p < .01$), but there is very little difference in mean birthweight between those with a full-blood father and those with a part-

TABLE 2

Means, Standard Deviations and Percentiles for
Birthweight (kg) of Queensland Children

Males					Percentiles				
Mother	Father	N	Mean	S.D.	5	25	50	75	95
Full	Full	60	3.003	.54	2.2	2.7	3.0	3.3	4.0
Full	Part	19	3.203	.40	2.4	2.9	3.3	3.5	3.8
Part	Full	15	3.301	.72	1.9	2.9	3.5	3.9	4.2
Part	Part	25	3.221	.42	2.6	2.8	3.3	3.4	3.9
Females									
Full	Full	46	2.879	.46	2.0	2.7	2.9	3.2	3.7
Full	Part	18	2.950	.58	1.9	2.5	2.9	3.4	4.1
Part	Full	17	3.228	.76	1.7	2.8	3.3	3.5	4.8
Part	Part	20	3.226	.58	2.3	2.7	3.3	3.7	4.0
Males									
Mother	Full	79	3.051	.52	2.3	2.7	3.1	3.3	4.0
Mother	Part	40	3.251	.55	2.1	2.8	3.4	3.6	4.1
Father	Full	75	3.063	.59	2.1	2.7	3.1	3.4	4.2
Father	Part	44	3.213	.41	2.6	2.8	3.3	3.5	3.8
Females									
Mother	Full	64	2.899	.49	2.0	2.6	2.9	3.2	3.7
Mother	Part	37	3.227	.66	2.3	2.7	3.3	3.7	4.2
Father	Full	63	2.973	.57	2.0	2.7	2.9	3.3	4.0
Father	Part	38	3.095	.59	2.3	2.7	3.0	3.6	4.1

blood father. This suggests that, although for both sexes the genes inherited from the mother play an important part in determining birthweight, the father's genes only assume importance in the case of males. That is, the Y-chromosome seems to carry genes which play a part in determining birthweight. This is consistent with the fact that the mean birthweight for boys is higher than that for girls. Furthermore, it appears that the presence of Caucasian genes in the mother leads to increased birthweight in female offspring, and the presence of Caucasian genes in either the mother or father leads to increased birthweight in male offspring.

Mean Weights, Heights and Head Circumferences

A mixed-longitudinal series of measurements from the three groups in the Northern Territory and two groups at Kowanyama were compared. The ten data sets obtained by dividing these five groups into males and females were found to be normally distributed using the UNISTAT1 computer program. The means, standard deviations and percentiles for these data are given in Appendices 1 (weight), 2 (height) and 3 (head circumference). The Student's t-test was used to test for significant differences between males and females, and full-bloods and part-bloods. At most ages, males are larger than females for each of the three measurements; the differences which are significant are shown in Table 3. At Milingimbi, there are very few significant differences, while for Maningrida and Kowanyama full-blood children, sex differences are significant at most ages for weight and head circumference, but are seldom significant for height. The mean head circumference for males is larger than that for females at most ages at Bathurst Island, and for ages up to 15 months, the same is true for

TABLE 3

Significant differences for sex for weight, height and head circumference

(Man. = Maningrida, B.I. = Bathurst Island, Mil. = Milingimbi, Kow. = Kowanyama)

Age	Weight			Height			Head Circumference		
	Man. B.I. Mil.	Kow. full part	Kow. full part	Man. B.I. Mil.	Kow. full part	Kow. full part	Man. B.I. Mil.	Kow. full part	Kow. full part
birth	**	-	**	-	-	*	-	-	-
1 mth	*	-	-	o	o	o	o	o	o
2 mth	**	-	-	o	o	o	o	o	o
3 mth	**	*	-	-	**	-	-	**	-
4 mth	**	*	-	o	o	o	o	o	o
5 mth	**	*	-	o	o	o	o	o	o
6 mth	**	-	-	**	**	-	-	**	-
9 mth	**	*	-	*	*	-	-	**	*
12 mth	**	**	-	-	**	*	-	**	**
15 mth	**	*	-	-	**	-	*	**	**
18 mth	**	-	-	-	-	-	*	**	**
21 mth	*	-	-	-	-	**	-	**	**
24 mth	**	-	-	-	*	*	-	**	**
30 mth	**	-	-	-	-	**	-	**	**
36 mth	-	-	-	-	-	**	-	**	-
42 mth	-	-	-	-	-	*	-	*	**
48 mth	-	-	-	-	-	-	*	**	-
* pr < .05 - not significant									
** pr < .01 o no data available									

weight and height. Sex-related differences among part-bloods at Kowanyama are also significant at most ages for head circumference, but for height and weight there are no significant differences until the age of 18 months. This contrasts with the full-blood populations where the majority of significant sex-related differences for weight and height are at ages less than 18 months. Part-bloods at Kowanyama have a larger mean weight, height and head circumference at most ages than full-bloods, but these differences are generally not significant. With regard to weight, full-blood and part-blood males are significantly different only at 24 months and 30 months, and females only at 9 months, while for height, full-blood males aged 36 months have a significantly different mean from that of part-blood males of that age (in each case, $p < .05$). There are no significant differences between full-bloods and part-bloods for head circumference. Thus, although mean head circumferences are significantly different at most ages between sexes, there are no significant differences between full-bloods and part-bloods.

To see whether or not the full-blood populations can be considered a homogeneous group a univariate analysis of variance was performed using the STATJOB analysis program ONEWAY1 (see Appendix 4). First, the four populations (three from the Northern Territory and one from Kowanyama) were tested, then the analysis was repeated using only the Northern Territory populations. Table 4 shows that at most ages the four populations cannot be considered to be a homogeneous group for weight, but when the Kowanyama population is removed the null hypothesis of homogeneity is almost always accepted; the only exceptions are for males at birth and females at one

TABLE 4

Homogeneity of the full-blood populations
for weight, height and head circumference

Age	Weight				Height				Head Circumference			
	Males		Females		Males		Females		Males		Females	
	1	2	1	2	1	2	1	2	1	2	1	2
birth	*	*	-	-	*	**	-	-	**	*	*	-
1 mth	**	-	**	*	o	o	o	o	o	o	o	o
2 mth	**	-	**	-	o	o	o	o	o	o	o	o
3 mth	*	-	**	-	*	-	*	-	*	-	-	-
4 mth	*	-	**	-	o	o	o	o	o	o	o	o
5 mth	**	-	**	-	o	o	o	o	o	o	o	o
6 mth	*	-	-	-	*	-	*	-	*	-	*	*
9 mth	**	-	*	-	-	-	-	-	**	-	*	-
12 mth	*	-	*	-	-	-	-	-	*	-	-	-
15 mth	*	-	*	-	-	-	-	-	*	-	-	-
18 mth	*	-	-	-	-	-	-	-	*	-	-	-
21 mth	*	-	*	-	-	-	-	-	*	-	-	-
24 mth	-	-	-	-	-	-	-	-	*	-	-	-
30 mth	*	-	*	-	-	-	-	-	*	-	-	-
36 mth	*	-	-	-	*	-	-	-	*	-	-	-
42 mth	-	-	*	**	*	-	-	-	*	-	-	-
48 mth	-	-	-	-	*	-	-	-	-	-	-	-

Group 1 = Kowanyama, Maningrida, Bathurst Island,
Milingimbi

Group 2 = Maningrida, Bathurst Island, Milingimbi

* pr < .05

** pr < .01

- not significant

o no data available

month and 42 months. It is interesting to note that at early ages Milingimbi children tend to be heavier than those at Bathurst Island, but after the age of six months the reverse occurs. For height and head circumference, the null hypothesis is also accepted more often when the Kowanyama group is removed, although, except for male head circumference, all four populations form a homogeneous group at most ages. Because of the homogeneity of the three Northern Territory populations, they have been combined to form one group for analysis of the mixed-longitudinal data.

In order to see the differences in mean growth among the populations, mean values have been plotted against age. Figure 1 shows the plots of male and female weight as a function of time for the Northern Territory group, Kowanyama full-bloods, Kowanyama part-bloods and, for further comparison, a white Australian group. The data for white Australians were obtained from the Australian Department of Health (1975). It is clear from this figure that male part-bloods at Kowanyama are heavier than full-bloods, and that Kowanyama full-bloods are heavier than Northern Territory males. These differences become very clear after about six months. At all ages the mean weight for the white males is higher than that for the part-bloods. In the case of females, the weights for the full-bloods and part-bloods at Kowanyama and Northern Territory full-bloods cluster together at all ages. After six months the white female children become much heavier than any of the Aboriginal female groups. Plots of height and head circumference as a function of age are shown in Figures 2 and 3, respectively. The height curves for males show a relationship similar to that seen in the weight curves, with full-blood Kowanyama

FIGURE 1

Mean Weights plotted against Age

Δ = Northern Territory, + = Kowanyama full-blood, ◐ = Kowanyama part-blood, no symbol = white

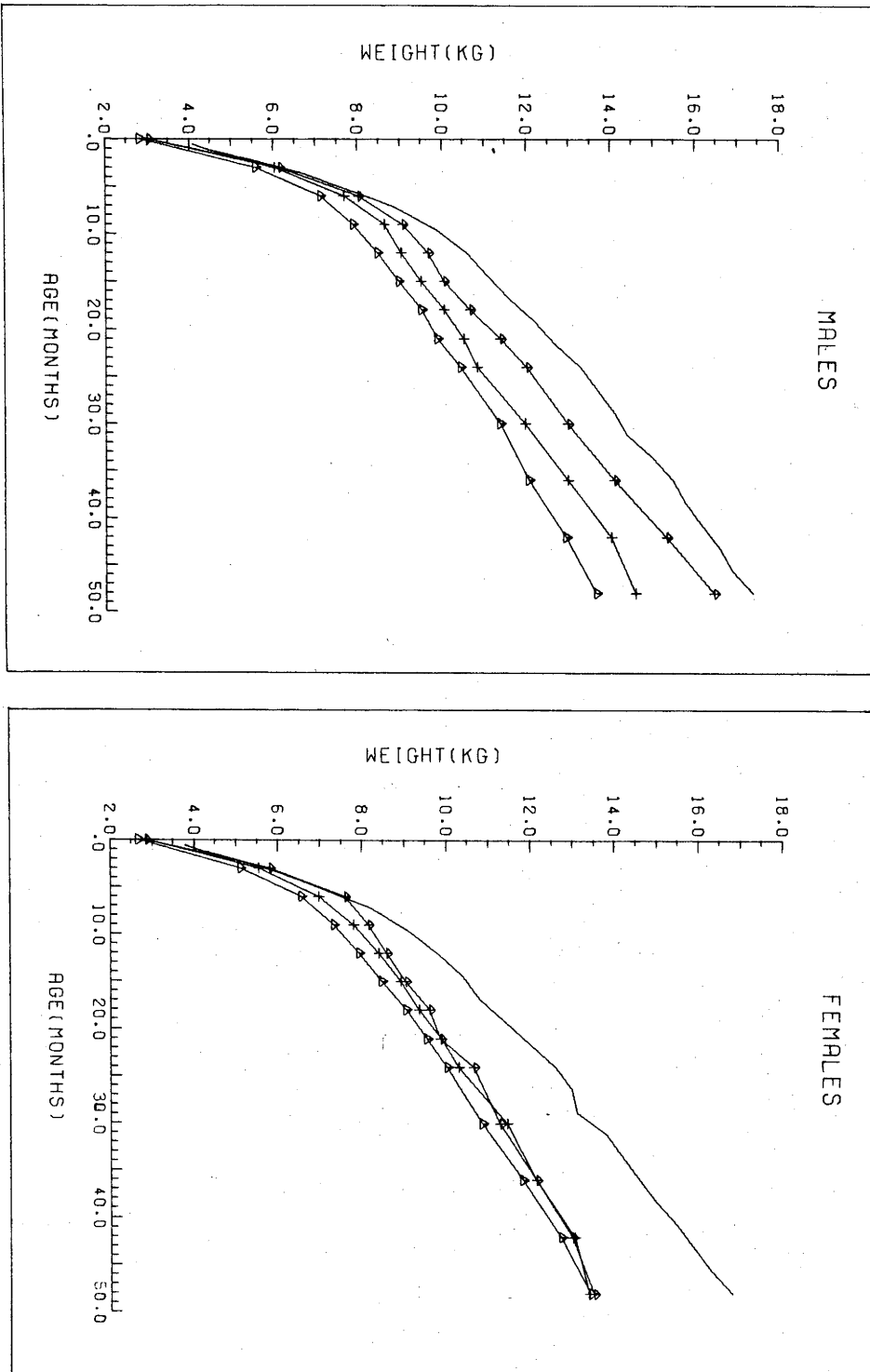


FIGURE 2
Mean Heights plotted against Age

Δ = Northern Territory, + = Kowanyama full-blood, ◀ = Kowanyama part-blood, no symbol = white

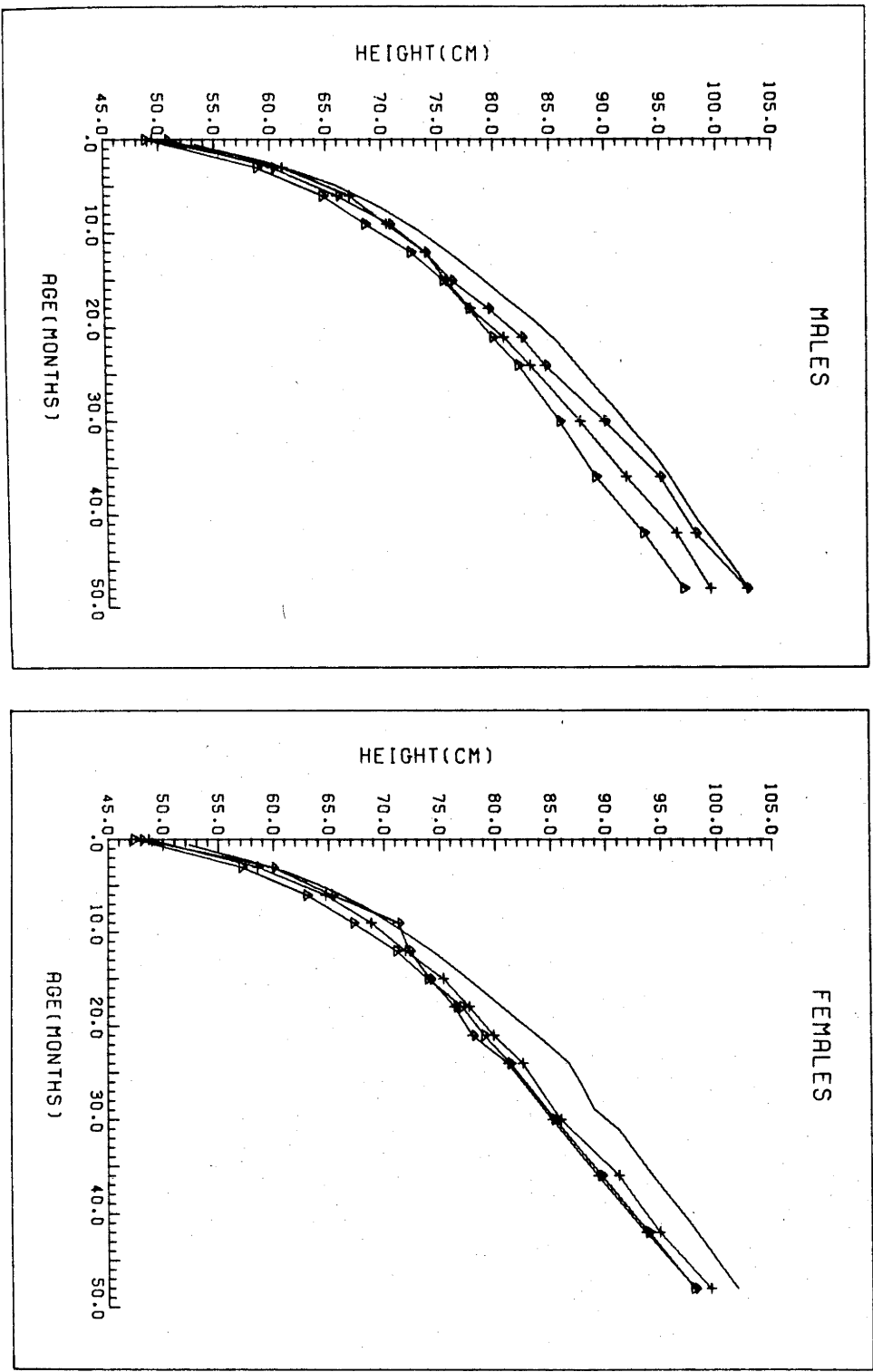
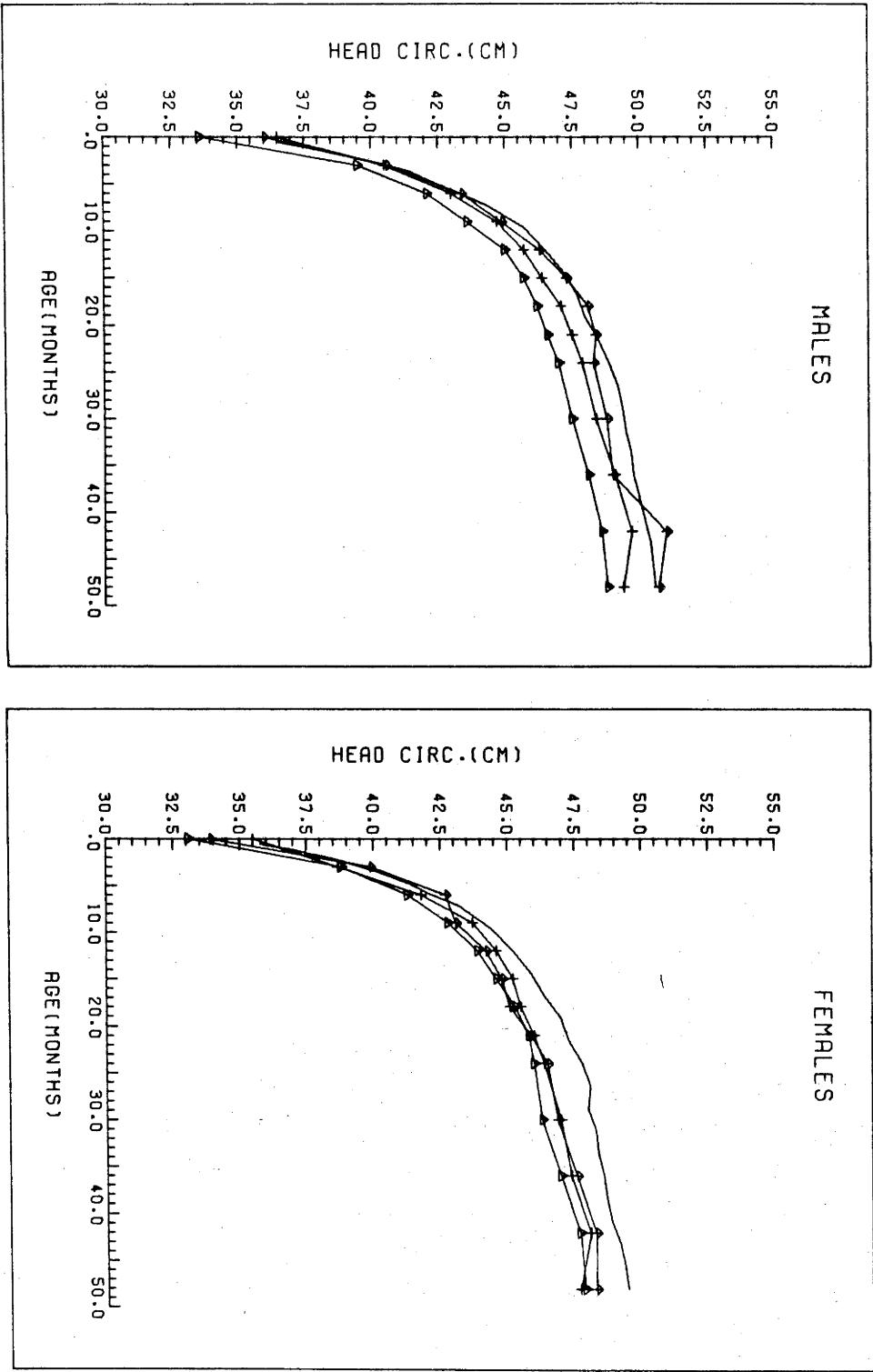


FIGURE 3
Mean Head Circumferences plotted against Age

Δ=Northern Territory, +=Kowanyama full-blood, ◄=Kowanyama part-blood, no symbol =white



males being taller than those in the Northern Territory, and part-blood Kowanyama males being taller than either full-blood group. The part-blood males are almost as tall as the white Australian males; in fact, their mean heights are almost identical at 48 months. The female Aboriginal groups have about the same mean height at all ages although for the first nine months the part-bloods are taller than the full-blood groups. For both weight and height, the part-blood females are close to the white females for the first six to nine months but after that they fall back to the level of the full-blood Aboriginal groups, while the white children continue to grow at a higher rate. For head circumference the patterns are similar. Although the male part-bloods have about the same mean head circumference as the white males at most ages, female part-bloods keep up with the white children only for the first few months after which they cluster with the full-blood populations.

Least-Squares Fit of a Polynomial to Growth Data

Fitting the polynomial $y = \alpha + \beta t + \gamma t^2$ to the weight, height and head circumference measurements at each age makes it possible to estimate whether the curves for different groups of children are significantly different from one another. This was done using the computer program POLFIT described by Bevington (1969) (see Appendix 4). The polynomial was fitted to each set of data separately and the values for the parameters and for the chi-square goodness of fit statistic are shown in Table 5. For weight, both α (initial value) and β (rate of increase) are higher in males than in females, while for height, the α values are always higher in males than in females, but not the β values, where Kowanyama full-bloods and whites show slightly higher

TABLE 5

Parameters of best fit of $y = \alpha + \beta t + \gamma t^2$ to growth data and chi-square goodness of fit (n = number of data points)

	Males				Females			
	α	β	γ	χ^2_{n-3}	α	β	γ	χ^2_{n-3}
WEIGHT								
Northern Territory	3.82	0.42	-.01	11.0	3.39	0.41	-.01	8.3
Kowanyama (full)	3.81	0.47	-.01	9.3	3.72	0.44	-.01	15.9
Kowanyama (part)	3.79	0.52	-.01	6.6	3.69	0.47	-.01	10.3
White	4.41	0.55	-.01	5.9	3.89	0.52	-.01	5.1
HEIGHT								
Northern Territory	53.9	1.60	-.02	6.1	52.4	1.58	-.01	5.1
Kowanyama (full)	53.9	1.65	-.02	4.6	52.2	1.69	-.02	7.8
Kowanyama (part)	54.1	1.69	-.02	3.3	52.5	1.56	-.01	6.4
White	55.7	1.83	-.02	6.6	53.8	1.84	-.02	6.4
HEAD CIRCUMFERENCE								
Northern Territory	37.0	0.69	-.01	14.4	36.9	0.60	-.01	9.8
Kowanyama (full)	37.9	0.68	-.01	6.8	38.7	0.52	-.01	6.1
Kowanyama (part)	37.8	0.69	-.01	5.9	38.2	0.52	-.01	6.3
White	39.0	0.64	-.01	8.9	38.0	0.62	-.01	9.6

rates of increase in females than in males. This pattern is reversed for head circumference with the initial value being higher for Kowanyama full-blood and part-blood females than for males, but the rate of increase is always higher for males than for females. For weight and height, α and β are both highest for the white children, but this is not so for head circumference. In all cases the chi-square values are not significant, indicating that the observed values are not significantly different from the polynomial fitted to the observations. By calculating chi-square values for two sets of data combined, it is possible to determine if the two data sets are significantly different from one another (see Appendix 4). The results of this test showed that for weight, male and female growth curves are significantly different only in the case of white children ($pr < .01$), while for height the differences between male and female curves are significant for Kowanyama part-bloods ($pr < .05$) and white children ($pr < .05$). For head circumference sex-related differences are significant for each of the four groups ($pr < .05$ for the Northern Territory and Kowanyama full-bloods and $pr < .01$ for the Kowanyama part-bloods and white children). There are no significant differences between full-bloods and part-bloods at Kowanyama of either sex for weight, height and head circumference. Similarly these differences between Northern Territory and Kowanyama full-bloods are not significant. However, the growth patterns of Northern Territory and white children are significantly different from one another ($pr < .01$) for each variable and sex. The Kowanyama full-blood growth patterns are also significantly different from those of white children ($pr < .01$ for weight and height), except for head circumference.

Males in the Northern Territory are significantly different from Kowanyama part-blood males for weight and height ($pr < .05$), but this is not so for females. On the other hand, Kowanyama part-blood females and white females have significantly different growth curves for each variable ($pr < .01$ for weight and height and $pr < .05$ for head circumference), but only weight and height differences are significant for males ($pr < .05$). It is clear that the differences between some of these growth curves are highly significant, particularly those between full-blood Aborigines in the Northern Territory and Kowanyama, and white children.

Relationships between Growth in Weight, Height and Head Circumference

In order to further examine the differences in growth curves, weight, height and head circumference have been plotted against one another for each group of children. Figure 4 shows mean height plotted against mean weight for males and females. After reaching a weight of about nine kilograms for boys and eight for girls, the white children tend to put on more weight relative to height increase than do the Aboriginal children. In each case the plots are approximately straight lines, with the gradient for the white children less than that for the Aboriginal children. Head circumference is plotted against weight for males and females in Figure 5. These graphs show that head circumference tends to level off as weight increases, and the mean head circumference at a particular weight is about the same for both white and Aboriginal groups. The main difference between the groups is that the white children and part-blood males have attained a larger weight by four years of age than have the full-bloods. The curves for height against head circumference in Figure 6

FIGURE 4
Mean Heights plotted against Mean Weights

Δ = Northern Territory, + = Kowanyama full-blood, ◐ = Kowanyama part-blood, no symbol = white

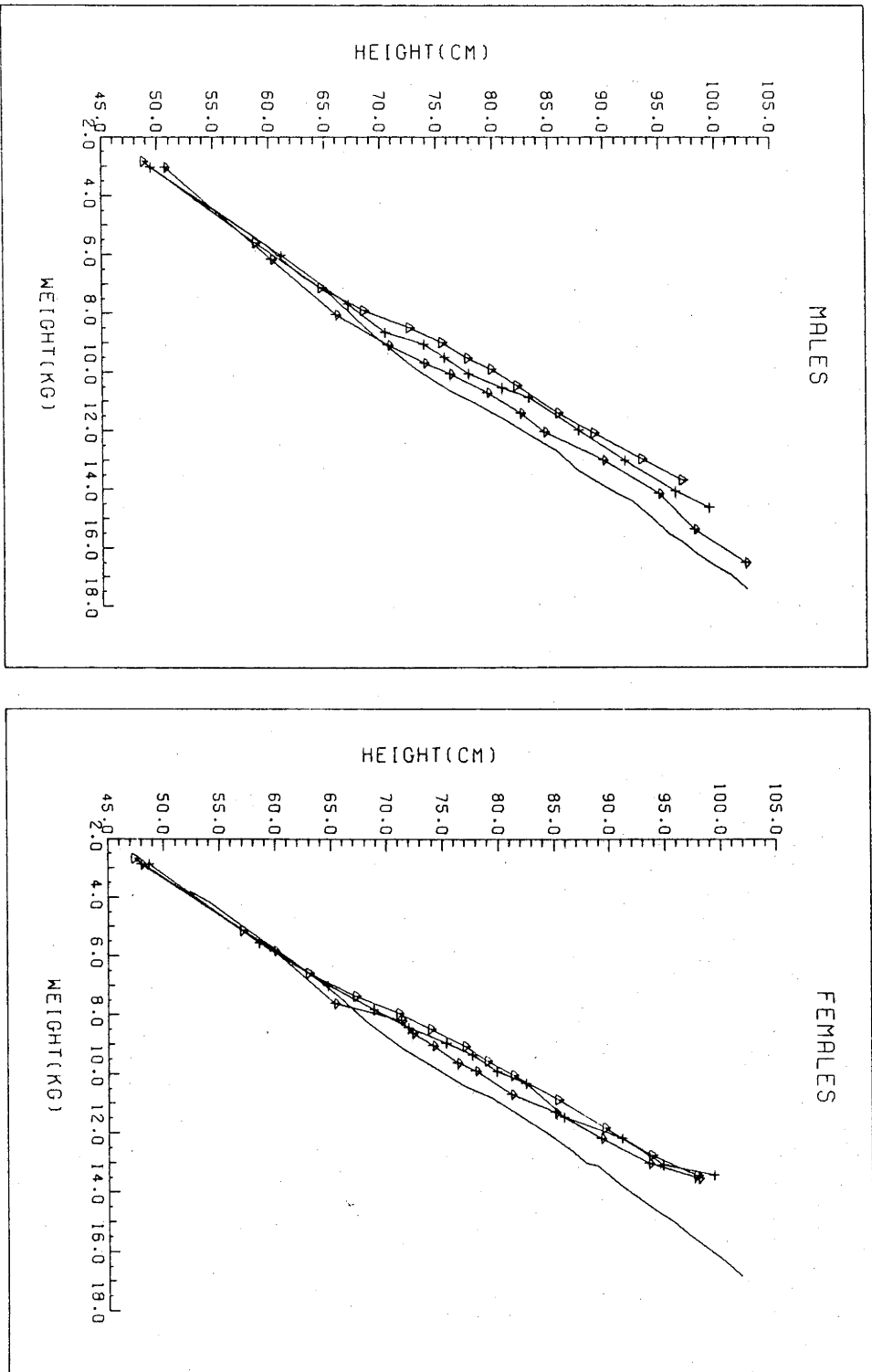


FIGURE 5

Mean Head Circumferences plotted against Mean Weights

Δ = Northern Territory, + = Kowanyama full-blood, ◄ = Kowanyama part-blood, no symbol = white

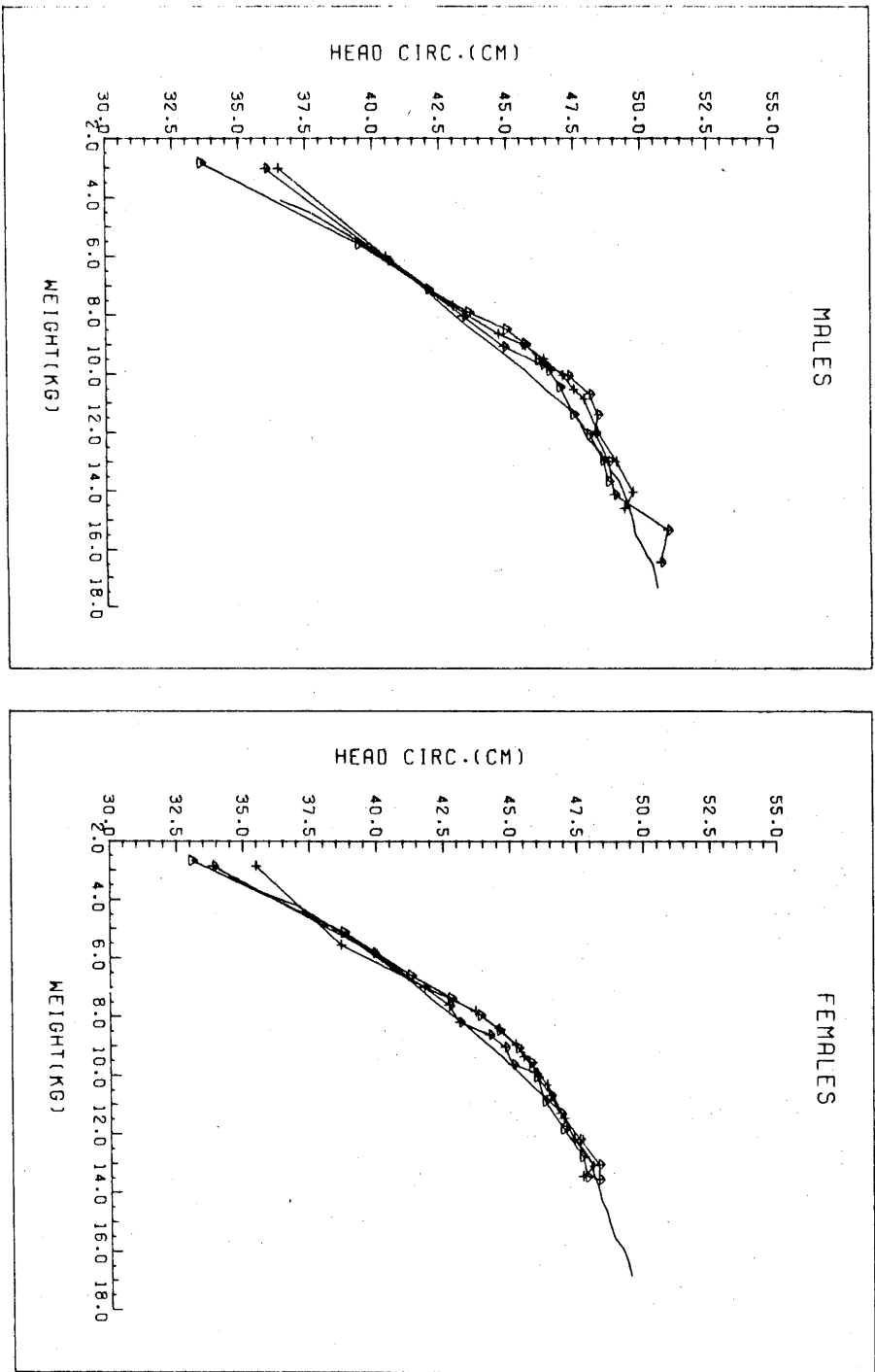
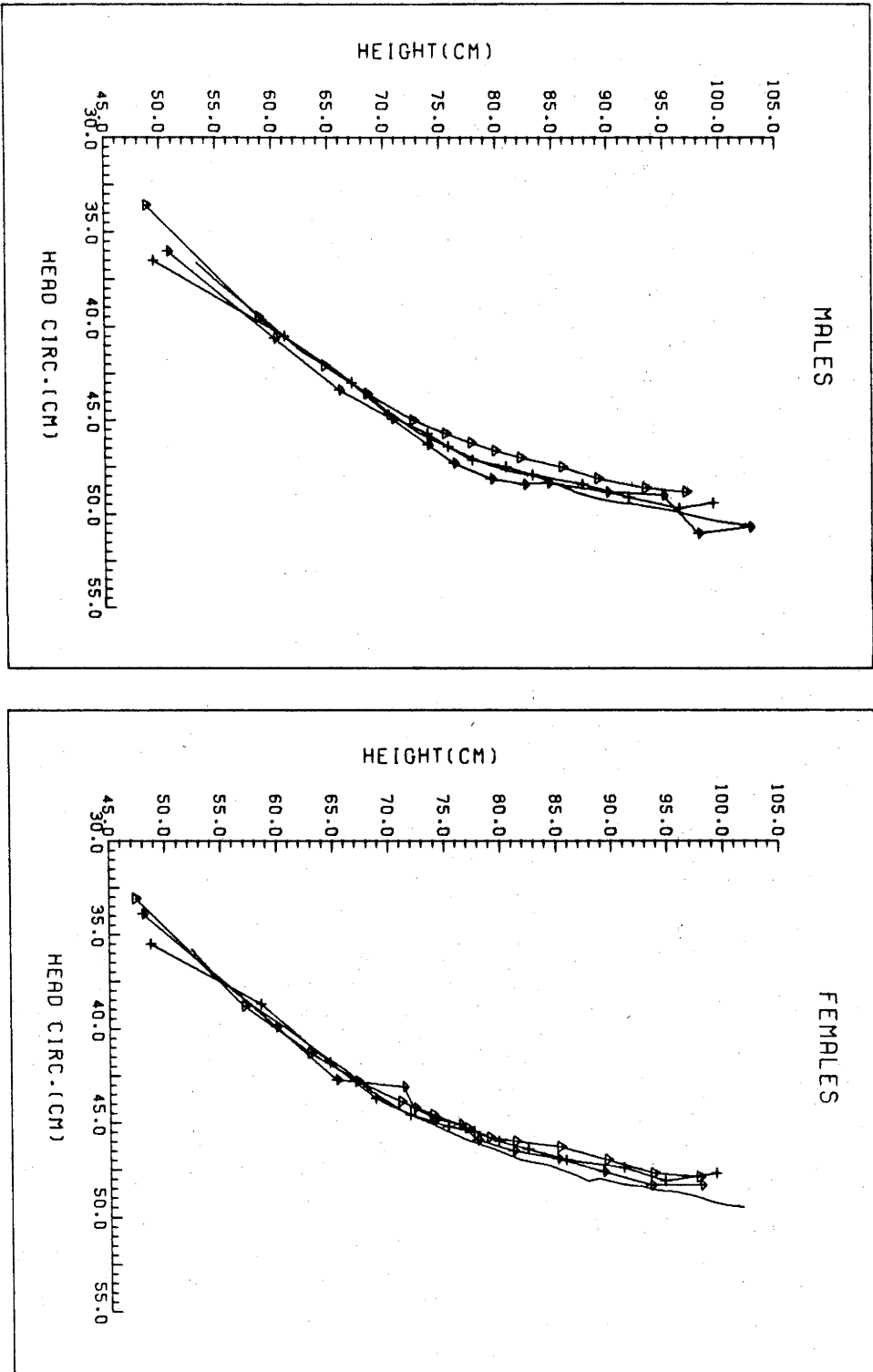


FIGURE 6

Mean Heights plotted against Mean Head Circumferences

Δ = Northern Territory, + = Kowanyama full-blood, ◄ = Kowanyama part-blood, no symbol = white



also tend to cluster together, with height increasing at a faster rate than head circumference. It therefore appears that growth in weight shows the main differences in growth patterns between Aboriginal and white children.

Another way of examining the relationships between different growth variables is to calculate the correlation coefficient between each pair. The STATJOB analysis program DSTAT2 (see Appendix 4) was used to obtain the correlation matrix for 39 variables (measurements at 13 ages between birth and four years for each of weight, height and head circumference). A contouring routine (see Appendix 4) was used to display the results from this analysis, and this technique was used for each set of variables against itself and against each other for the Northern Territory, Kowanyama full-blood and Kowanyama part-blood children. The highest correlations were found when a set of variables was paired with itself, with the highest correlations occurring between ages which were close to one another. Figure 7 shows the contours of correlations between weights at different ages, heights at different ages and head circumferences at different ages for males in the Northern Territory and part-blood males at Kowanyama. In the case of the Kowanyama sample, several areas of random fluctuation may have been introduced by the small sample size. However, the trends are similar for both sets of data. The correlations between weight at birth and weights at later ages fall off fairly quickly. The same relationship is observed for height and head circumference at birth. However, after birth, the correlations between weight at a particular age and weights at later ages decrease much more slowly than do these correlations for height and

head circumference. This occurs for all of the sets of data, though the part-blood males have a larger area of high correlations than do the full-bloods. This trend is also seen in Figure 8, which shows the contours for weight against height, weight against head circumference and height against head circumference. The highest correlations are found along the diagonal where the ages are the same for the two variables. For the Northern Territory data these values are about 0.5, while for the Kowanyama part-bloods values of 0.7 to 0.8 are found.

The analyses of Aboriginal growth data suggest that full-bloods and part-bloods grow differently from one another, and from white children during the first four years of life. The next chapter deals with the question of whether these differences are simply nutritional, or whether genetic differences can be inferred from the growth patterns.

FIGURE 7

Contours of Correlations between weights at different ages, heights at different ages, and head circumferences at different ages (small nos. inside axes denote correlation; axes give age in months)

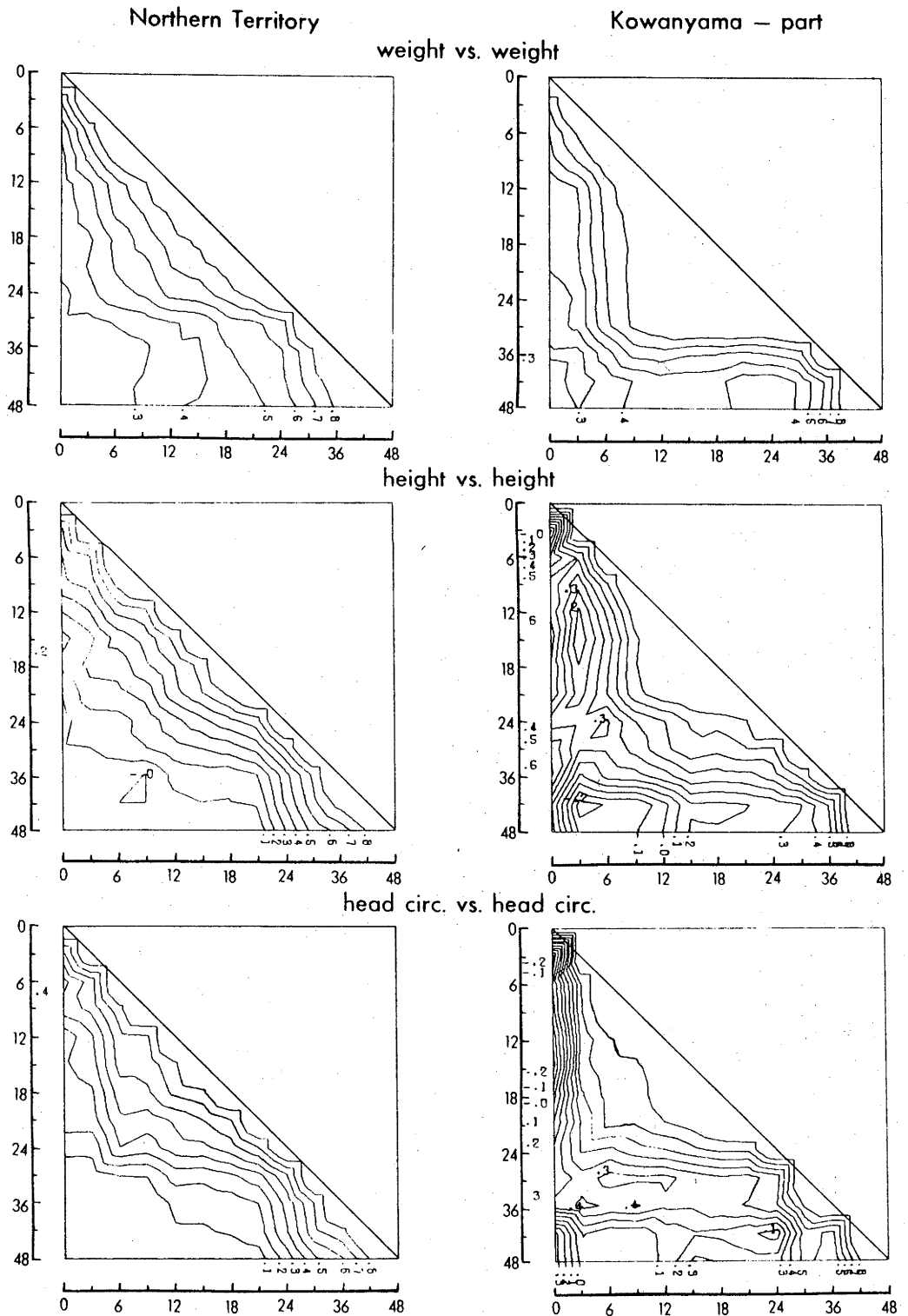
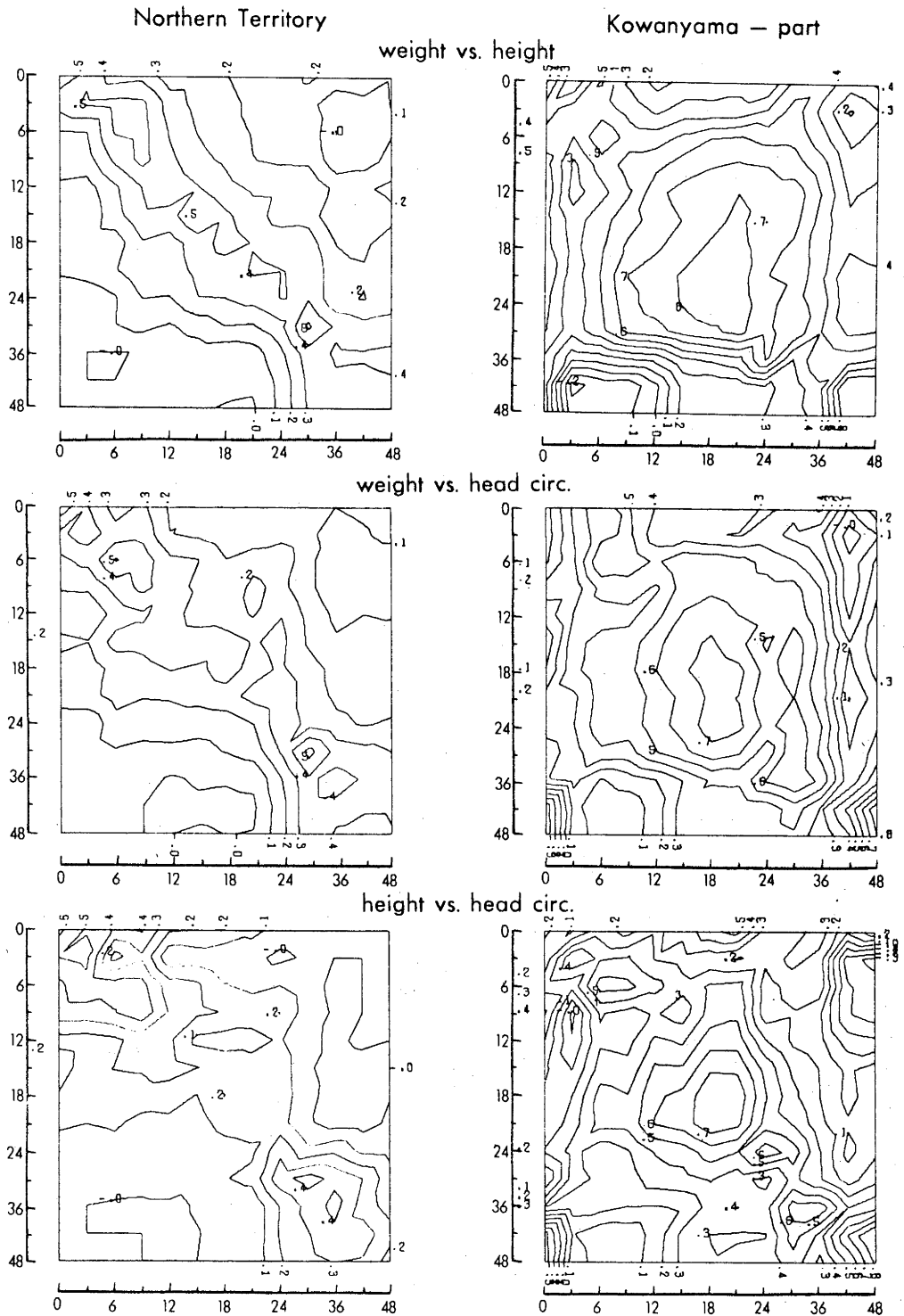


FIGURE 8

Contours of Correlations between weight and height,
weight and head circumference, and height and head
circumference (small nos. inside axes denote correlation;
axes give age in months)



Chapter 4

NUTRITION AND THE GENETIC CONTROL OF GROWTH IN
AUSTRALIAN ABORIGINAL CHILDREN

Growth is a continuous process which is to some extent genetically controlled. However, adequate nutrition is very necessary for the genetic growth potential to be attained. Aborigines are genetically different from the white population, and by white standards Aboriginal nutrition is inadequate; both factors must contribute to the low growth rates observed in Aboriginal children. It may be that genetically Aborigines require less food than whites to maintain their energy balance, and consequently the growth pattern of Aboriginal children is different from that of white children.

Nutritional Status

Growth measurements have been used as an index of the nutritional status of a community. In 1966, Jelliffe set out standards for growth variables at different ages. Weight, weight for height, and weight for head circumference of Aboriginal children have been compared with these standards. The percentage of Aboriginal children falling below standard for birthweight are classified in Table 6. For each sample of children more than 50% have birthweights above 80% of the standard, with a few birthweights below 60% of standard. According to Jelliffe (1966), children below 60% of the standard are suffering from severe protein-calorie malnutrition. However, the low birthweights may simply reflect the high premature birth rate among Aborigines.

TABLE 6

Percentages of Children in Different Percentage
Classes of Standard Birthweight

Males

<u>Males</u>		Percent of Standard				
Full-bloods	N	≥90	80-89	70-79	60-69	<60
Northern Territory	158	48	23	18	6	5
Kowanyama	35	54	20	17	9	0
Queensland	60	54	23	12	8	3
Kimberley	156	56	23	13	6	2
Part-bloods						
Kowanyama	23	53	17	22	4	4
Queensland	59	69	19	7	3	2
Kimberley	101	72	17	8	2	1

Females

Full-bloods						
Northern Territory	145	28	26	26	14	6
Kowanyama	30	37	43	13	7	0
Queensland	46	41	33	15	7	4
Kimberley	123	52	20	19	7	2
Part-bloods						
Kowanyama	16	38	25	25	6	6
Queensland	55	53	25	9	9	4
Kimberley	102	62	23	10	5	0

The majority of Queensland children with either full or part-blood parents have birthweights above 80% of the standard (Table 7). The results listed in Table 7 are consistent with those given in Table 2 with both results suggesting that the father's genes on the Y-chromosome play a part in determining male birthweight, but only the mother's genes are important with respect to female birthweight.

Growth before birth is remarkably resistant to under-nutrition of the mother (Ounsted and Ounsted, 1973) which suggests that birthweight is not a good measure of the nutritional status of the community. Measurements taken after birth probably provide a more accurate measure of the nutritional status. Table 8 shows the distribution of levels below standard, for weight, weight for height, and weight for head circumference, for children in the Northern Territory and at Kowanyama. Data taken at six months and data averaged over the period 12 to 48 months are given for weight, while the values for weight for height and weight for head circumference are the averages over all ages. For weight, the percentage of children above 90% of standard is higher at six months than at birth, but decreases to a much lower value between 12 and 48 months. At birth and six months the percentage of full-blood males and females above 90% of standard is about the same as that of part-bloods. However, between 12 and 48 months the percentage of part-bloods at this level is considerably higher than that of full-bloods. It is interesting to note that this is true for females, even though the mean weight values for full-blood and part-blood females at Kowanyama are about the same. This is a result of the fact that among the part-bloods there are more females whose weights are

TABLE 7

Percentages of Queensland Children in Different
Percentage Classes of Standard Birthweight

<u>Males</u>			Percent of Standard				
Mother	Father	N	≥90	80-89	70-79	60-69	<60
Full	Full	60	54	23	12	8	3
Full	Part	19	68	22	5	5	0
Part	Full	15	73	7	7	7	6
Part	Part	25	68	24	8	0	0
<u>Females</u>							
Full	Full	46	41	33	15	7	4
Full	Part	18	44	22	17	11	6
Part	Full	17	53	29	6	6	6
Part	Part	20	60	25	5	10	0
<u>Males</u>							
Mother	Full	79	57	23	10	8	2
Mother	Part	40	70	18	8	2	2
Father	Full	75	57	20	11	8	4
Father	Part	44	68	23	7	2	0
<u>Females</u>							
Mother	Full	64	42	30	16	8	5
Mother	Part	37	57	27	5	8	3
Father	Full	63	44	32	13	6	5
Father	Part	38	53	24	10	10	3

TABLE 8

Percentages of Children in Different Percentage Classes
of Standard Weight, Weight for Height, and Weight for
Head Circumference

<u>Weight: 6 months</u>		Percent of Standard				
Males	N	≥90	80-89	70-79	60-69	<60
Northern Territory	132	70	24	5	1	0
Kowanyama Full-bloods	33	85	9	6	0	0
Kowanyama Part-bloods	22	77	18	5	0	0
Females						
Northern Territory	120	50	29	15	3	3
Kowanyama Full-bloods	28	67	29	4	0	0
Kowanyama Part-bloods	13	69	31	0	0	0
<u>Weight: 12-48 months</u>						
Males						
Northern Territory	298	26	49	24	1	0
Kowanyama Full-bloods	70	45	41	11	3	0
Kowanyama Part-bloods	38	68	21	8	3	0
Females						
Northern Territory	277	13	44	36	7	0
Kowanyama Full-bloods	61	21	48	31	0	0
Kowanyama Part-bloods	29	34	28	31	7	0
<u>Weight for Height</u>						
Males						
Northern Territory	773	64	32	4	0	0
Kowanyama Full-bloods	266	69	24	5	1	1
Kowanyama Part-bloods	152	79	20	1	0	0
Females						
Northern Territory	603	54	39	7	0	0
Kowanyama Full-bloods	216	54	40	5	1	0
Kowanyama Part-bloods	97	68	26	5	1	0
<u>Weight for Head Circum.</u>						
Males						
Northern Territory	636	90	9	1	0	0
Kowanyama Full-bloods	202	80	15	4	1	0
Kowanyama Part-bloods	113	76	18	6	0	0
Females						
Northern Territory	533	93	6	1	0	0
Kowanyama Full-bloods	178	93	4	2	0	1
Kowanyama Part-bloods	85	93	6	1	0	0

above 90% of standard, but there are also more whose weights are below 70% of standard, than among full-blood females. This suggests that after six months of age the diet of some of the part-blood females is not adequate, but that this is not so for males. In all cases, the percentage of Northern Territory children in the first level below the standard is lower than that of either full-blood or part-blood Kowanyama children.

The results for weight for height and weight for head circumference show that almost all of the children are above 80% of the standard. In the case of weight for height the percentage of part-bloods in the first level below the standard is higher than that of full-bloods for both males and females. In other words, more full-bloods than part-bloods are below the standard weight for their height. However, weight for head circumference results show that in the case of males more part-bloods than full-bloods are below the standard weight for head circumference. This suggests that the head circumferences of part-blood males tend to be large (there was only one individual whose head circumference for age fell below 90% of standard). In the case of females, almost all of the children are above 90% of standard weight for head circumference. Height for age and head circumference for age were above 80% of standard for all children with the majority of the children above 90% of standard. Therefore, weight for age is the main indicator of different growth patterns for Aboriginal children from those for white children. According to Jelliffe (1966), these results would suggest that a large number of the children are suffering from mild to moderate protein-calorie malnutrition (those between 60% and 90% of standard). Similarly, the growth index defined by Jose and Welch (1970) suggested that

about the same proportion of the children are growth retarded. The differences between full-bloods and part-bloods, however, indicate that genetic differences may be as important as nutrition in explaining the differences between growth patterns of Aborigines and white children.

Resemblance between Relatives: Measurements at Birth

One method for examining the genetic component of growth measurements is to analyse these measurements for genetically related individuals. The intraclass correlation coefficient (see Appendix 4) measures the degree of resemblance between relatives, and it is used for this purpose.

Birthweight data for sib pairs were obtained from the Northern Territory, Kowanyama, Queensland and the Kimberley. Birth-length and birth-head circumference data were available for some sib pairs as well. The intraclass correlation coefficient calculated for each set of data is shown in Table 9. For birthweight the coefficient is about 0.5 for each group, but for birth-length and head circumference at birth it is lower. This suggests that sibs are more similar in birthweight than in the two other measurements. In all cases, except for the Queensland birthweight data, the intraclass correlation coefficient for male sibs is higher than that for either female sibs or male-female sib pairs. This would be expected if the Y-chromosome plays an important part in determining birthweight, because male sibs have the same Y-chromosome. These results are seen most clearly for birthweight in the Northern Territory and the Kimberley. The trends are similar for Kowanyama birthweight, and birth-length and birth-head circumference in the Northern Territory but the sample sizes are small, which reduces the reliability of the correlation coefficients.

TABLE 9

Intraclass Correlations Between Sibs

Full-Sibs								
	Total	Female	Male	Male-Female				
BIRTHWEIGHT								
Northern Territory	322	.5342	68	.4013	96	.6567	158	.4607
Kowanyama	61	.4572	10	-.1798	17	.4734	34	.4074
Queensland	153	.5912	33	.6596	47	.3938	73	.6443
Kimberley	288	.5445	73	.5307	78	.5526	139	.5426
BIRTHLENGTH								
Northern Territory	39	.2659	13	.1046	15	.3457	11	.2279
Kowanyama	23	.2655	-	-	-	-	-	-
BIRTH HEAD CIRCUMFERENCE								
Northern Territory	37	.3993	12	.3205	15	.7088	10	.0339

Negative values are obtained when the birthweights of pairs of sibs fall on opposite sides of the mean birthweight over all pairs. The reason for the much larger correlation coefficients for female and male-female sibs than for male sibs in the Queensland sample is not clear. It may be that these birthweights are inaccurate, or that random environmental effects on birthweight have affected the Queensland data more than those from the Northern Territory and the Kimberley.

Genealogical data for Kowanyama were used to determine birthweights of cousin pairs. Table 10 shows the intraclass correlation coefficients for different types of cousin pairs for birthweight and birth-length. Neither of the values for all cousins are significant. When this set of all cousin pairs is separated into subsets based on either the sexes of the related parents or the sexes of the cousins, the correlation coefficients for birth-length are negative, but have a greater magnitude than those for birthweight; this may be a result of the small sample sizes for birth-length. There were enough cousin pairs in the case of birthweight to divide the data into subsets based on the sexes of the related parents and the cousins. The highest correlation was obtained for sons of brothers. This again suggests that genes on the Y-chromosome are important in determining male birthweight, since the same Y-chromosome is passed from the brothers to their sons.

If birthweight was completely genetically determined by autosomal additive genes then the sib pair correlations would be 0.5 and the cousin pair correlations would be 0.125. The values obtained in the analysis of Aboriginal birthweight show a great deal of variation, and it could not be concluded that birthweight is controlled only by autosomal additive genes.

TABLE 10

Correlations Between Cousins at Kowanyama
(Br. = Brother; Sis. = Sister)

	Birthweight		Birthlength	
All cousins	353	.0567	56	-.1833
Children of Br.	63	.2021	6	-.2873
Children of Sis.	135	.0008	30	-.3149
Children of Br. & Sis.	155	-.0129	20	-.0727
Daughters of Sibs	111	.1548	15	-.5112
Sons of Sibs	75	.1102	9	-.5991
Son & Daughter of Sibs	167	-.0199	32	-.0643
Daughters of Br.	16	.0498	-	-
Sons of Br.	17	.5360	-	-
Son & Daughter of Br.	30	.0457	-	-
Daughters of Sis.	45	.0346	-	-
Sons of Sis.	25	.1451	-	-
Son & Daughter of Sis.	65	-.1261	-	-
Daughters of Br. & Sis.	50	.2390	-	-
Sons of Br. & Sis.	33	-.3579	-	-
Son & Daughter of Br. & Sis.	72	-.0252	-	-

Other factors such as the intrauterine environment of the mother are likely to contribute to the birthweight of a child, and these factors would tend to reduce the correlation coefficient. However, the analysis of Aboriginal birthweight suggests that chromosomes inherited from the mother and, in the case of male children, the Y-chromosome inherited from the father, are important in determining the birthweight of the child.

Time Series Analysis of Growth Data

Growth before birth is likely to be determined by different genes from those controlling growth after birth because of the importance of the mother in prenatal growth. In order to analyse growth after birth it is useful to be able to summarize the growth curve of each individual using as few parameters as possible. Each individual growth curve is a time series, that is, a set of data points describing a process at several points in time. The methods of time series analysis described by Box and Jenkins (1970) have been used to identify and fit a model to each set of growth data, and to forecast future values of the time series. This was done using a package of computer programs developed at the University of Wisconsin and the Ohio State University for the analysis of univariate time series models using the methods of Box and Jenkins (1970) (see Appendix 4).

Growth is not a statistically stationary process because its mean and variance change with time, but it may be reduced to a stationary process by taking differences of the observed values. To test whether the model can be fitted by an autoregressive process, a moving average process or a mixture of both (see Appendix 4), autocorrelations of different lags were calculated. Examples of the autocorrelations and partial

autocorrelations for weight, height and head circumference are shown in Table 11 for up to three differences and five lags. A second difference model was chosen because the autocorrelation is insignificant for lags greater than zero. Several models involving one or two autoregressive and/or moving average parameters were tested. The one which gave the closest fit and best predictions was a (1,2,0) model. That is, an autoregressive process of order 1 for the second difference of the equally-spaced observations $Z_t, t=1, \dots, 9$ was used. This may be written as

$$(1 - \phi B) (1 - B)^2 Z_t = a_t$$

where ϕ is the autoregressive parameter and B is an operator such that $BZ_t = Z_{t-1}$. In this model the current value of the process is expressed as a finite, linear aggregate of the previous values of the process and a random shock a_t , and from it, future values may be predicted. Table 12 gives examples of fitted values and forecasts for weight, height and head circumference. Despite the fact that only nine data points were available, the fitted value is very close to the data value. Similarly, the forecast values are close to the actual values not used in the computations. The (1,2,0) model, therefore, provides an accurate description of human growth for weight, height and head circumference.

Using nine equally spaced data points covering the ages from birth to two years, the ARIMA (1,2,0) model was fitted to weight, height and head circumference data for as many individuals as possible from the Northern Territory and Kowanyama. The mean parameter values for each sample of individuals are shown in Table 13. Although the standard deviations are high, all of the parameter values fell in the

TABLE 11
Autocorrelations and Partial Autocorrelations
(in brackets)
L A G

Weight					
Original Series					
1st difference	1	2	3	4	5
2nd difference	.54±.33(.54)	.21±.42(-.11)	.05±.43(-.03)	-.11±.43(-.15)	-.24±.43(-.15)
3rd difference	.43±.35(.43)	-.10±.41(-.36)	-.07±.42(.20)	-.08±.42(-.24)	-.19±.42(-.06)
	.05±.38(.05)	-.18±.38(-.19)	-.09±.39(-.07)	-.04±.39(-.07)	-.20±.40(-.24)
	-.48±.41(-.48)	-.09±.49(-.41)	.00±.50(-.40)	.09±.50(-.29)	-.03±.50(-.27)
Height					
Original Series					
1st difference	1	2	3	4	5
2nd difference	.58±.33(.58)	.27±.43(-.10)	.04±.45(-.11)	-.12±.45(-.11)	-.25±.45(-.15)
3rd difference	.49±.35(.49)	.17±.43(-.09)	-.20±.44(-.33)	-.35±.45(-.15)	-.33±.48(-.04)
	.34±.38(.34)	.17±.42(.06)	-.20±.43(-.31)	-.27±.44(-.15)	-.39±.46(-.23)
	-.43±.41(-.43)	-.06±.48(-.30)	-.14±.48(-.40)	.43±.49(.21)	-.30±.54(-.05)
Head Circumference					
Original Series					
1st difference	1	2	3	4	5
2nd difference	.49±.33(.49)	.23±.40(-.01)	-.01±.42(-.15)	-.15±.42(-.11)	-.22±.42(-.11)
3rd difference	.25±.35(.25)	.22±.37(.17)	-.05±.39(-.15)	-.27±.39(-.30)	-.29±.41(-.17)
	-.20±.38(-.20)	.04±.39(-.00)	.09±.39(.10)	-.06±.40(-.03)	-.25±.40(-.29)
	-.35±.41(-.35)	-.17±.45(-.32)	.12±.46(-.09)	.15±.47(.14)	-.25±.48(-.13)

TABLE 12

Fitted Values and Forecasts

Age(mth)	Fitted Value	Residual	Data Value
<u>Weight</u>			
9	10.7	-1.5	9.2
12	9.3	0.5	9.8
15	10.4	0.1	10.5
18	11.2	-0.1	11.1
21	11.7	-0.2	11.5
24	11.9	0.0	11.9
<u>Height</u>			
9	68.7	0.3	69.0
12	73.6	-1.6	72.0
15	74.2	-0.2	74.0
18	75.6	0.4	76.0
21	78.0	1.2	79.2
24	82.9	-0.5	82.4
<u>Head Circ.</u>			
9	44.3	0.2	44.5
12	47.0	-1.8	45.8
15	47.2	-1.2	46.0
18	46.3	-0.1	46.2
21	46.4	0.6	47.0
24	47.8	-0.3	47.5
Age(mth)	Forecast	95% Confidence Limits	Actual Value
<u>Weight</u>			
27	12.3	10.9 - 13.7	-
30	12.7	9.1 - 16.3	12.8
33	13.1	6.8 - 19.4	-
36	13.5	4.0 - 23.0	14.3
<u>Height</u>			
27	85.6	83.7 - 87.5	-
30	88.8	83.9 - 93.7	87.5
33	92.0	83.1 - 100.9	-
36	95.2	81.4 - 109.0	93.0
<u>Head Circ.</u>			
27	48.0	46.4 - 49.6	-
30	48.5	45.1 - 52.0	48.0
33	49.1	43.4 - 54.7	-
36	49.6	41.4 - 57.8	48.8

range from -1 to +1, and each set was approximately normally distributed. For some individuals, parameter values representing weight, height and head circumference were obtained and the correlations between these three variables are shown in Table 14. None of these correlations are significant, which suggests that the growth pattern of Aborigines for one variable cannot be used to indicate their growth pattern for either of the other two variables.

Resemblance between Relatives: Growth Parameters

Parameter values obtained from the time series analysis for weight of sib and cousin pairs were analysed, and the intraclass correlation coefficients are given in Table 15. The sib pair correlations are lower than those determined for birth-weight indicating that random environmental factors are more important after birth. Further, the correlation for female sibs is higher than that for male sibs, which agrees with the suggestion that females are less likely than males to be removed from their genetic course of growth by environmental factors (Tanner, 1962). The highest correlations among cousin pairs are for daughters of sisters and daughters of a brother and a sister, which again shows the tendency for girls to stick more closely to their genetic pattern of growth than do boys.

Although the Aboriginal children do not reach the growth standards of white children, particularly in weight, the correlations between relatives are often quite high. These correlations are, of course, due to both genetic and environmental similarities of relatives. However, the fact that the intraclass correlation coefficient seems to depend on the sexes of the relatives suggests that genetic similarity may be

TABLE 13
Mean Parameters

	Weight			Height			Head Circumference		
	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
<u>Males</u>									
Northern Territory	75	-.0302	.3187	31	-.1000	.3508	30	.0019	.2885
Kowanyama Full-bloods	26	-.0083	.3345	9	.0907	.2849	-	-	-
Kowanyama Part-bloods	14	.1734	.2203	5	-.0977	.2976	-	-	-
<u>Females</u>									
Northern Territory	70	-.0640	.3672	23	-.1350	.2619	23	.0338	.2217
Kowanyama Full-bloods	21	-.0423	.3754	3	.0054	.1731	-	-	-
Kowanyama Part-bloods	8	-.0829	.3730	-	-	-	-	-	-

TABLE 14
Correlations between Weight, Height and Head Circumference

	Weight vs. Height		Weight vs. Head Circ.		Height vs. Head Circ.	
Northern Territory Males	30	0.229	30	-0.050	30	0.114
Northern Territory Females	23	-0.022	23	0.248	23	-0.029
Kowanyama	17	0.053	-	-	-	-

TABLE 15
Correlations Between Sibs and Cousins for Weight Parameters

	Northern Territory	Kowanyama
All sibs	118 -.0575	26 .1736
Male sibs	30 .0466	- -
Female sibs	24 .2011	- -
Male-Female sibs	64 -.2164	- -
All cousins	- -	110 .0119
Children of brothers	- -	20 -.0284
Children of sisters	- -	46 -.1171
Children of brother & sister	- -	44 .1199
Daughters of sibs	- -	27 .0785
Sons of sibs	- -	23 -.0418
Son & Daughter of sibs	- -	60 -.0452
Daughters of brothers	- -	- -
Sons of brothers	- -	- -
Son & Daughter of brothers	- -	13 -.0091
Daughters of sisters	- -	12 -.5455
Sons of sisters	- -	9 -.2777
Son & Daughter of sisters	- -	25 -.0763
Daughters of brother & sister	- -	13 .3354
Sons of brother & sister	- -	9 -.0863
Son & Daughter of brother & sister	- -	22 -.0631

more important than environmental similarity. It appears that genetic control of weight is more important before birth than after birth when random nutritional differences among children tend to over-rule their genetic pattern of growth, although this occurs more for boys than for girls.

Chapter 5

DISCUSSION OF GROWTH IN AUSTRALIAN ABORIGINAL CHILDREN

Growth studies of Aboriginal children from many parts of Australia have shown that their birthweights and weights at various ages after birth are lower than those found for white children. Similar results have been found for height and head circumference. In most cases the low values have been attributed to the poor nutrition of Aboriginals. Genetic differences, however, certainly occur between Aboriginal and white populations, and it seems likely that some of the growth differences are due to genetic factors.

The mean birthweights of 2.8 kg for males and 2.7 kg for females in the Northern Territory obtained in this study are lower than the mean value of 2.9 kg for both males and females obtained by Kettle (1966) for Arnhem Land children. Similarly the mean birth-lengths of 48.8 cm for males and 47.4 cm for females are lower than Kettle's (1966) values of 49.8 cm for males and 49.5 cm for females. However, both weights and heights after birth are very similar to those obtained by Kettle (1966). The mean birthweights for Queensland of 3.0 kg for males and 2.9 kg for female full-bloods are the same as those for Kowanyama, but are lower than the values of 3.3 kg for males and 3.1 kg for females given by Propert *et al.* (1968) for Mornington Island full-bloods. However, the mean weights for Kowanyama full-bloods at 12 months of age of 9.1 kg for males and 8.4 kg for females are close to the mean weights of 9.0 kg for males and 8.4 kg for females obtained for Mornington Island by Propert *et al.* (1968) for children aged 360 days. Propert *et al.* (1968) also give mean birthweights

for full-bloods and part-bloods in Western Australia. Their values of 3.0 kg for male and female full-bloods are about the same as the values of 3.1 kg for males and 3.0 kg for females obtained in this study. Similarly, their values of 3.3 kg for male and 3.2 kg for female part-bloods are close to the values of 3.3 kg for male and 3.1 kg for female part-bloods obtained for the Kimberley children. Thus, the results obtained in this study agree with previously published results from the same areas. In addition, this study indicates variation in measurements of weight, height and head circumference for Aborigines living in different parts of Australia.

There are two main reasons for this variation; genetic differences and nutritional differences. In comparing Aboriginal growth with that of white children it is obvious that additional factors such as climate and socio-economic conditions would contribute to variation in growth. However, the effects of these environmental factors would not be as great among the Aboriginal communities used in this study, particularly for full-bloods and part-bloods living in the same communities.

The analysis of the birthweight data for Queensland and Kimberley children suggests that genetic differences may be responsible for the fact that part-bloods are heavier than full-bloods. However, birthweights of Kowanyama females show that other factors such as adequate nutrition must also be involved. It may be that there is a threshold level for required food intake, which is genetically determined and is higher for part-bloods than for full-bloods and higher again for white children. Genetic determination of nutritional intake has also been suggested by Widdowson (1962) and Mayer and Thomas

(1967). In the case of the Kowanyama part-blood females this level is not reached and so their growth falls below that which would be expected. It is known that in Aboriginal societies the males are given the best food while the females eat what remains, so it is possible that the food supply is above the threshold for both part-blood and full-blood males and full-blood females, but it is not adequate to meet the genetically determined needs of part-blood females. It is suggested, therefore, that to attain genetic potential in growth, the level of nutrition must be above a genetically determined threshold.

Further evidence of the genetic factors involved in growth is obtained from the analysis of birthweights of Queensland children. The fact that mean birthweight for males is larger than that for females suggests that the Y-chromosome inherited from the father plays a part in determining the birthweights of males. In addition, the Queensland results suggest that only the chromosomes inherited from the mother affect female birthweight because the mean birthweight for children with a part-blood mother is significantly higher than that for children with a full-blood mother, whereas the mean birthweights are about the same for females with a full-blood and part-blood father. For the males, however, the mean birthweights are higher whenever there are part-blood genes present whether they are from the father or the mother. Thus the genes on the chromosomes inherited from the mother plus the Y-chromosome inherited from the father in the case of males are the major factors controlling intrauterine growth and birthweight of the child. The importance of the genes on the Y-chromosome is again seen by the facts that the intraclass correlation

coefficient for male sibs is generally larger than that for female sibs or male-female sibs, and the highest correlation for cousins is for sons of brothers.

Genetic factors are also important for growth after birth. Sex-related differences are an example of this, and they are most evident for head circumference, although there are significant differences between males and females for weight and height. It is interesting to note that for full-bloods most of the significant differences occur before the age of 18 months, whereas for part-bloods sex-related differences tend to be significant only after 18 months of age. Other evidence of genetic effects on growth is the higher correlations between weight, height and head circumference (see Figures 7 and 8) found for part-bloods than for full-bloods.

The time series analysis of growth data shows that a second difference autoregressive model can be fitted to growth data, and that predictions of growth close to actual values can be obtained. This technique of analysis provides a parameter value which summarizes an individual growth curve, and should prove to be a powerful analytic technique especially when a large number of equally spaced data points are available. The sib pair and cousin pair correlations for these parameters are lower than for birthweight indicating that environmental factors tend to dominate the genetic control of growth after birth. The higher correlations for female relatives agree with the suggestion that environmental effects are less likely to change the growth pattern of females than of males (Tanner, 1962).

The results of this analysis of growth of Australian Aboriginal children support the fact that growth is to a large

extent genetically controlled provided that nutrition is maintained at or above some threshold level. In addition, it is suggested that the Y-chromosome transferred from the father plays an important part in determining male size at birth, while the genes inherited from the mother are major factors in the control of both male and female intrauterine growth.

This study suggests several techniques for the analysis of the genetic and environmental components of growth variables. It is clear that the study of full-blood and part-blood Aborigines living in the same environment can provide important information concerning the effect of genetic factors on growth. This is particularly true when it is known whether the parents of the children studied are full-blood or part-blood. Data on parents available for this study limited the analysis to prenatal effects on birthweight. Similar studies using measurements of continuous characteristics taken after birth are certainly required to increase our understanding of the importance of inherited factors in determining these characteristics. The analysis of family data indicates genetic control of birthweight. The hypothesis that the Y-chromosome transferred from the father to the son has significant control over birthweight needs to be tested further by analysis of birthweights of relatives such as parent and child. The power of time series analysis of continuous characteristics can only be realized if more, equally spaced data points are available, and future experimental programs should take these sampling requirements into account. The collection of more family data will also make possible the type of analysis applied by Rao *et al.* (1975) to height and weight measurements from Northeastern Brazil. It appears that accurate and frequent collection of the growth measurements of

Aboriginal children will provide data which are most useful in increasing our understanding of the roles played by genetics and the environment in determining growth patterns.

PART II

POPULATION STRUCTURE IN INDIGENOUS PEOPLES OF
AUSTRALIA AND NEW GUINEA

Chapter 6

GENETIC DIFFERENTIATION: INTRODUCTION AND TECHNIQUES

In Part I the quantitative characteristics of height, weight and head circumference were used to infer genetic factors in the control of growth rates. In this section qualitative markers in the blood which are completely controlled by genes are used to determine genetic relationships between geographically separated populations. The results from this technique are shown to be consistent with, and perhaps more sensitive than, relationships inferred from linguistic studies of these populations.

Distances based on quantitative measurements

Many different methods have been suggested for measuring differentiation among populations; they are reviewed by Chakraborty (1975) and Balakrishnan *et al.* (1975). Attempts to define coefficients to measure the biological distance between populations were first made towards the end of the 19th century. In 1926, Pearson described his Coefficient of Racial Likeness (C.R.L.) which he used for measuring resemblances between samples of skulls from various origins. Anthropologists have since used this measure for classifying skeletal remains (Sokal and Sneath, 1963). Penrose (1954) considered both size and shape differences in defining his measures of differentiation for continuous characteristics. However these coefficients ignore correlations between the variables being studied. The first measure to take into account both the variance of the separate characteristics and the correlations among characteristics was the Generalized Distance statistic,

D^2 , defined by Mahalanobis in 1936. He assumed that the variables were normally distributed within each population with a common covariance matrix, V , and defined the generalized distance between two populations as

$$D_{mn}^2 = (X_m - X_n)^T V^{-1} (X_m - X_n) \quad (6.1)$$

where $X_m = (X_{1m}, X_{2m}, \dots, X_{pm})$ and $X_n = (X_{1n}, X_{2n}, \dots, X_{pn})$ represent the vectors of the mean values of p variables for the m^{th} and n^{th} populations, respectively.

This measure has been used for a large number of anthropometric surveys to determine the relationships between populations based on continuous characteristics (e.g. Mahalanobis *et al.*, 1949; Majumdar and Rao, 1958).

However, these measures for quantitative characteristics cannot be applied to qualitative data such as genetic markers in the blood since the assumption of normal distribution does not hold.

Distances based on qualitative measurements

In 1953 Sanghvi developed an index for determining genetic distances between populations based on discrete variables. It is related to the chi-square statistic. This index was modified by Balakrishnan and Sanghvi (1968) who also proposed two new indices for qualitative characteristics which are extensions of Mahalanobis' (1936) generalized distance statistic.

A different approach to measuring genetic distance was taken by Cavalli-Sforza and Edwards (1967). In this case, suppose that q_{ijm} represents the frequency of the i^{th} allele

at the j^{th} locus in the m^{th} population. The vector of gene frequencies $(q_{1jm}, q_{2jm}, \dots, q_{rjm})$ may be transformed to $(\sqrt{q_{1jm}}, \sqrt{q_{2jm}}, \dots, \sqrt{q_{rjm}})$ so that each population can be denoted by a point on the surface of a unit hypersphere (one quadrant of a circle for a two-allele locus and, in general, a $1/2^r$ section of an $(r-1)$ dimensional hypersurface for r alleles). The angular distance in radians between two populations, m and n at the j^{th} locus, is then given by α_{jmn} where

$$\cos \alpha_{jmn} = \sum_i \sqrt{q_{ijm}} \sqrt{q_{ijn}} \quad (6.2)$$

The distance between the populations is an arc α_{jmn} units in length. Cavalli-Sforza and Edwards (1967) introduced a constant factor $2/\pi$ so that the distance $(2\alpha_{jmn}/\pi)$ has a value of one for a complete gene substitution. They preferred to convert this distance to the length of the chord, and defined their genetic distance measure as

$$d_{jmn} = \frac{2}{\pi} \sqrt{2(1 - \cos \alpha_{jmn})} \quad (6.3)$$

Since the distance between populations for each locus is assumed to be independent they can be combined such that the square of the distance between two populations is given by the sum of the squared distances between them for each locus. That is, the genetic distance between the m^{th} and n^{th} populations is given by

$$d_{mn} = \frac{2}{\pi} \sqrt{2 \sum_j (1 - \cos \alpha_{jmn})} \quad (6.4)$$

Of course, by approximating the arc distance to the length of the chord, the distance for a complete gene substitution is no longer one, but 0.90.

In 1971, Morton *et al.* suggested that measures of genetic distance should be biologically meaningful; they considered the concept of identity by descent as a measure of the relationships between populations, and termed the procedure "Bioassay of Kinship": The theory of kinship has developed from the foundation of Wright's (1943) Hierarchical model. Morton (1973a, b, and c) has discussed the definition of kinship and the information which can be obtained from it concerning population structure. Kinship is defined as the correlation between uniting gametes relative to the contemporary gene pool. It is equivalent to the Wahlund variance (Cavalli-Sforza and Bodmer, 1971), and may be calculated from the formula

$$\phi_{jmn} = \frac{H_o - H_{jmn}}{H_o} = \frac{\sum_i q_{ijm} q_{ijn} - \sum_i Q_{ij}^2}{1 - \sum_i Q_{ij}^2} \quad (6.5)$$

where $H_{jmn} = 1 - \sum_i q_{ijm} q_{ijn}$ is the heterozygosity of an F_1 population derived from populations m and n , and $H_o = 1 - \sum_i Q_{ij}^2$ is the heterozygosity of the regional population formed from all of the populations being analysed (that is, the contemporary gene pool). Q_{ij} is the regional frequency of the i^{th} allele at the j^{th} locus and q_{ijm}, q_{ijn} are the frequencies of the i^{th} allele at the j^{th} locus in populations m and n , respectively.

If $H_o > H_{jmn}$ then ϕ_{jmn} may be considered to be the probability that a random gene in m is identical by descent with a random gene in n . The kinship value will be high if H_{jmn} is much lower than H_o . On the other hand, it will be negative if the regional population shows less variation than the F_1 of populations m and n ; this indicates that a contemporary gene

pool with greater heterozygosity is required before any genes in m and n can be considered identical by descent. Therefore, it is possible that two populations which are not related with respect to one regional population may show significant relationship for a larger regional population which contains more variation. However, increasing the number of populations included in the analysis does not necessarily increase the variation in the regional population, so kinship may decrease when the size of the regional population is increased.

Morton *et al.* (1971) found that a more efficient, unbiased estimator of kinship is provided by

$$\phi_{jmn} = \{ \sum_i (q_{ijm} q_{ijn} / Q_{ij}) - 1 \} / (h_j - 1) \quad (6.6)$$

where h_j is the number of alleles at the j^{th} locus.

They also define a function of kinship called hybridity which measures the dissimilarity between populations by comparing the heterozygosity in an F_1 population with that in an F_2 . It is defined as

$$\theta_{jmn} = \frac{H_{jmn} - H_{j,m+n}}{H_{j,m+n}} = \frac{\phi_{jmm} + \phi_{jnn} - 2\phi_{jmn}}{4 - 2\phi_{jmn} - \phi_{jmm} - \phi_{jnn}} \quad (6.7)$$

where $H_{j,m+n} = 1 - \sum_i (q_{ijm} + q_{ijn})^2 / 4$ is the heterozygosity in the F_2 population from populations m and n .

The kinship and hybridity over all loci may be calculated by taking the mean weighted according to sample size. The formulae are

$$\phi_{mn} = \frac{\sum_i W_{jmn} \phi_{jmn}}{\sum_i W_{jmn}} \quad (6.8)$$

$$\text{and} \quad \theta_{mn} = \frac{\sum_i W_{jmn} \theta_{jmn}}{\sum_i W_{jmn}} \quad (6.9)$$

where $W_{jmn} = (N_{jm} + N_{jn})/2$, and N_{jm} , N_{jn} are the sample sizes for the j^{th} locus in populations m and n , respectively.

A dissimilarity index similar to hybridity has been suggested by Latter (1973). Instead of measuring the excess of heterozygosity in an F_1 population relative to an F_2 , he considered the mean heterozygosity for two populations relative to that predicted in the F_1 population and defined his measure as

$$\phi_{jmn}^* = \frac{H_{jmn} - H_{j,m,n}}{H_{jmn}} \quad (6.10)$$

where $H_{j,m,n} = 1 - \frac{\sum_i (q_{ijm}^2 + q_{ijn}^2)}{2}$ is the mean level of heterozygosity within populations m and n .

This index is related to hybridity by the expression

$$\phi_{jmn}^* = \frac{2\theta_{jmn}}{1 + \theta_{jmn}} \quad (6.11)$$

The mean value over all loci is obtained by calculating the mean values of H_{jmn} and $H_{j,m,n}$ and is given by

$$\phi_{mn}^* = 1 - \frac{\sum_j H_{j,m,n}}{\sum_j H_{jmn}} \quad (6.12)$$

Cavalli-Sforza (1969) defined another measure which can be related to hybridity. Using the angular distance α_{jmn} as defined in Equation 6.2 the function is defined as

$$f_{\alpha_{jmn}} = \frac{4(1 - \cos \alpha_{jmn})}{h_j - 1} \quad (6.13)$$

It is equivalent to twice the square of d_{jmn} (as defined in Equation 6.3) ignoring the constant factor $2/\pi$, weighted by the number of alleles at locus j , (h_j). Morton (1973a) shows that it is related to hybridity by

$$f_{\alpha_{jmn}} (h_j - 1) = 4[1 - q^2 - q(1-q)^2 \alpha_{jmn} - (1-q)^2 - q(1-q)^2 \alpha_{jmn}] \quad (6.14)$$

$$\text{where } q = (q_{ijm} + q_{ijn})/2$$

Cavalli-Sforza and Bodmer (1971) claim that $f_{\alpha_{jmn}}$ measures kinship. However, the fact that its upper limit is 4 and that its value increases as populations become less similar make it unacceptable as a measure of kinship. The mean value of $f_{\alpha_{jmn}}$ over all loci can be written

$$f_{\alpha_{mn}} = \frac{4 \sum_j (1 - \cos \alpha_{jmn})}{\sum_j (h_j - 1)} \quad (6.15)$$

The concept of identity of genes within and between populations was also considered by Nei (1971, 1972) as a genetic distance measure. He proposed an index which is equivalent to normalized kinship, assuming that the homozygosity of the reference population (Q_{ij}^2) is zero. In 1973, Nei justified this by the argument that "the number of alleles at a locus in a population is expected to vary from time to time, and the alleles existing at one evolutionary time may be different from those at another". In applying a homozygosity value of zero to electrophoretic data he assumes that the reference population is very large (for example, an infinite population in which neutral mutations are occurring at an infinite number of codons, or a population consisting of many different species, in which a particular allele is present in only a small number of the species) (Morton, 1973a). The value of zero may be meaningful when different species are being compared, but not when comparisons within species are being made. Wright (1973) maintains that the homozygosity value should vary according to the populations being analysed.

Nei's (1971, 1972) measure of genetic similarity may be

written as

$$I_{jmn} = \frac{\sum_i q_{ijm} q_{ijn}}{\sum_i q_{ijm}^2 \sum_i q_{ijn}^2} = \frac{J_{jmn}}{J_{jm} J_{jn}} \quad (6.16)$$

which is equivalent to

$$I_{jmn} = \frac{\phi_{jmn}}{\phi_{jmm} \phi_{jnn}} \quad (6.17)$$

assuming that $Q_{ij}^2 = 0$.

From this measure Nei (1971) defined a standard index of genetic distance with respect to all loci as

$$D_{mn} = -\log_e \left\{ \frac{\sum_j J_{jmn}}{\sum_j J_{jm} \sum_j J_{jn}} \right\} \quad (6.18)$$

Values of ϕ^* (Latter, 1973), θ (Morton *et al.*, 1971), f_α (Cavalli-Sforza, 1969), D (Nei, 1971, 1972) and d (Cavalli-Sforza and Edwards, 1967) for a subset of the data used in this study are given in Appendix 5. Each of these measures provides a similar picture of the relationships between this set of populations, but, as shown above, they are all related in some manner to kinship. As Morton (1973a) states, "except for the regional inbreeding α , all the information about population structure in any generation is contained within the square, symmetrical matrix of pairwise random kinship. Any further analysis, to describe isolation by distance, evolution of kinship, or genetic topology is an operation on this matrix. Except for α no other index, which is not an operation on this matrix, provides additional information about population structure". Kinship as defined by Morton *et al.*, (1971) is therefore used for the remaining analyses of the indigenous populations of Australia and New Guinea in this study.

The methods of topology which may be applied to the kinship matrix are discussed by Lalouel (1973). It is often

desirable to be able to present the relationships between populations in two dimensions. This means, in general, that the positions of the populations relative to one another are not accurately represented, because a maximum of $N-1$ dimensions may be required to plot the distances between N populations.

However, a two-dimensional representation does provide a useful summary of the kinship matrix, and its accuracy may be assessed by the cophenetic correlation coefficient R (Sokal and Rohlf, 1962) where R is equal to one if the representation provides an accurate picture of the kinship matrix, and decreases as the relationships become less accurately presented. Lalouel (1973) describes several methods for representing the relationships between populations in two dimensions. Two of these methods are used in this study: the eigenvector and the dendrogram (or tree) representation. For the former, the first and second eigenvectors of the kinship matrix are plotted against one another, while the dendrogram is an hierarchical representation of the populations derived from cluster analysis, such that the most similar populations are grouped together.

Kinship values generally show variation among loci. This may be due to differences in selection coefficients or mutation rates. A high mean kinship at a locus indicates that the regional homozygosity is much lower than the mean homozygosity, which implies that there are marked differences in gene frequencies between some of the populations. A low value of mean kinship indicates that there is not much variation among populations at that locus.

The relationship between kinship and geographic distance was derived by Malecot (1969). He showed that kinship relative to an original (founder) population is given approximately by

$$\phi_{mn} \approx ae^{-bd} \quad (6.19)$$

where d is the distance between populations m and n .

However, "Bioassay of Kinship" gives the kinship value relative to the contemporary regional gene pool, and Morton (1973a and b) has shown that a useful description of population structure is obtained by a least-squares fit of the equation

$$\phi(d) = (1 - L)ae^{-bd} + L \quad (6.20)$$

to the kinship data. The parameters may be interpreted as

- (i) local kinship (a);
- (ii) the exponential decline with distance (b); and
- (iii) the kinship as distance becomes very large (L).

Chapter 7

GENETIC DIFFERENTIATION: POPULATIONS SAMPLED

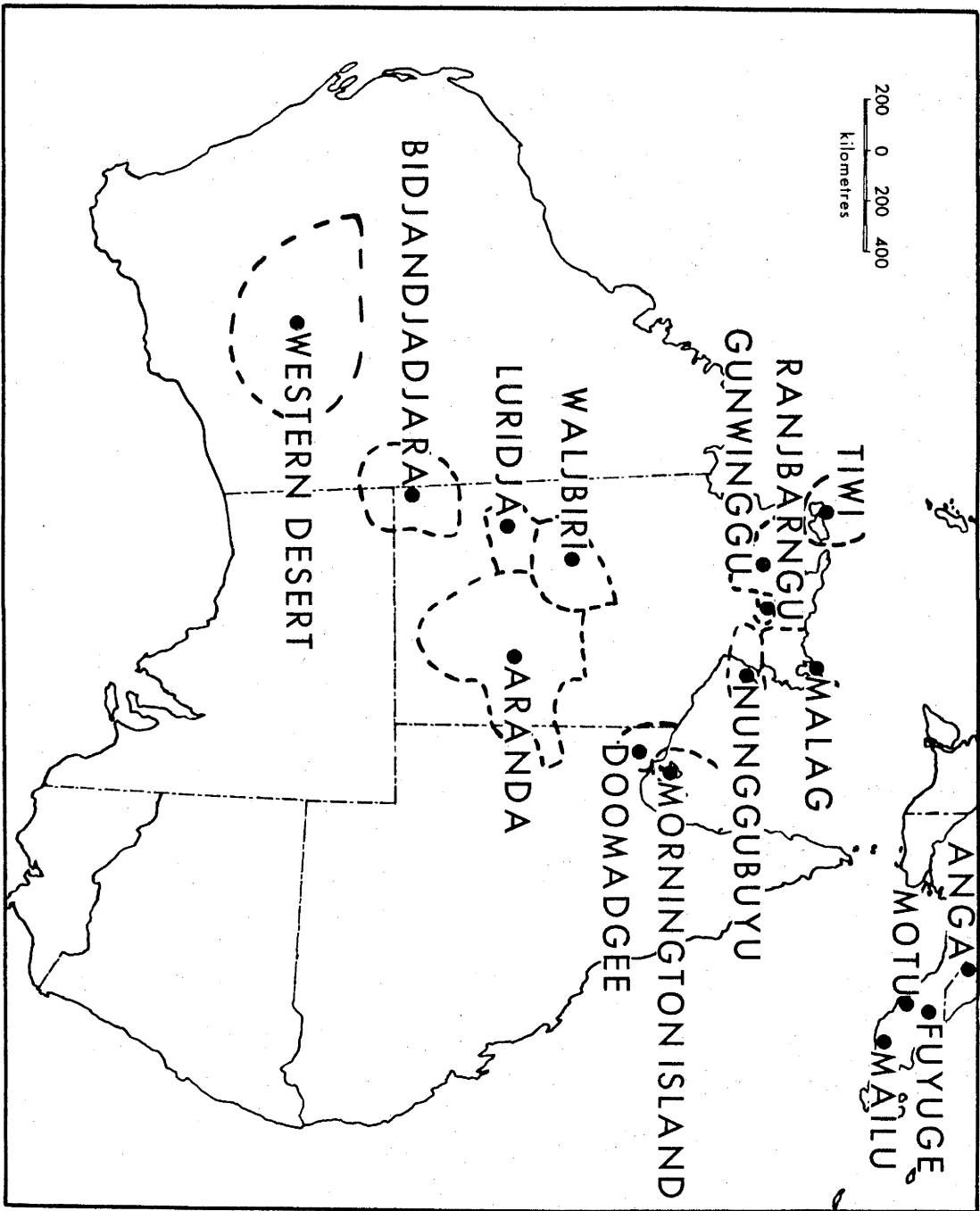
Twelve populations from Australia have been used for this study, nine from the Northern Territory, two from Queensland and one from Western Australia (Map 2). The Northern Territory populations and the one from Western Australia each represent speakers of a single language; speakers of several different languages are included in the two Queensland populations. In Papua New Guinea (Map 3) eight populations from the highlands, and for contrast, two populations from the south-east coastal area, two from Karkar Island just north of Madang, and two from the Admiralty Islands were used. A more distinct population of Melanesians from Fiji was also included to see if Melanesian genetic relationships are distinguishable over greater distances of separation by sea. Each of the populations in Papua New Guinea, the Admiralty Islands and Fiji is composed of speakers of a single language. This group of populations will be referred to as the Eastern New Guinea data set. From Western New Guinea (Map 3) five populations have been used, two from the highlands and three from coastal or river plains. The people included in each population speak languages belonging to the same language family.

Australia

The inland areas of the Northern Territory and Western Australia are primarily desert areas. There is a central zone of ranges running east-west for 500 to 650 kilometres from which water courses flow, and beside which grassy plains are found. However, the lowlands on either side of these hills are covered by sand and spinifex, and water is difficult to obtain

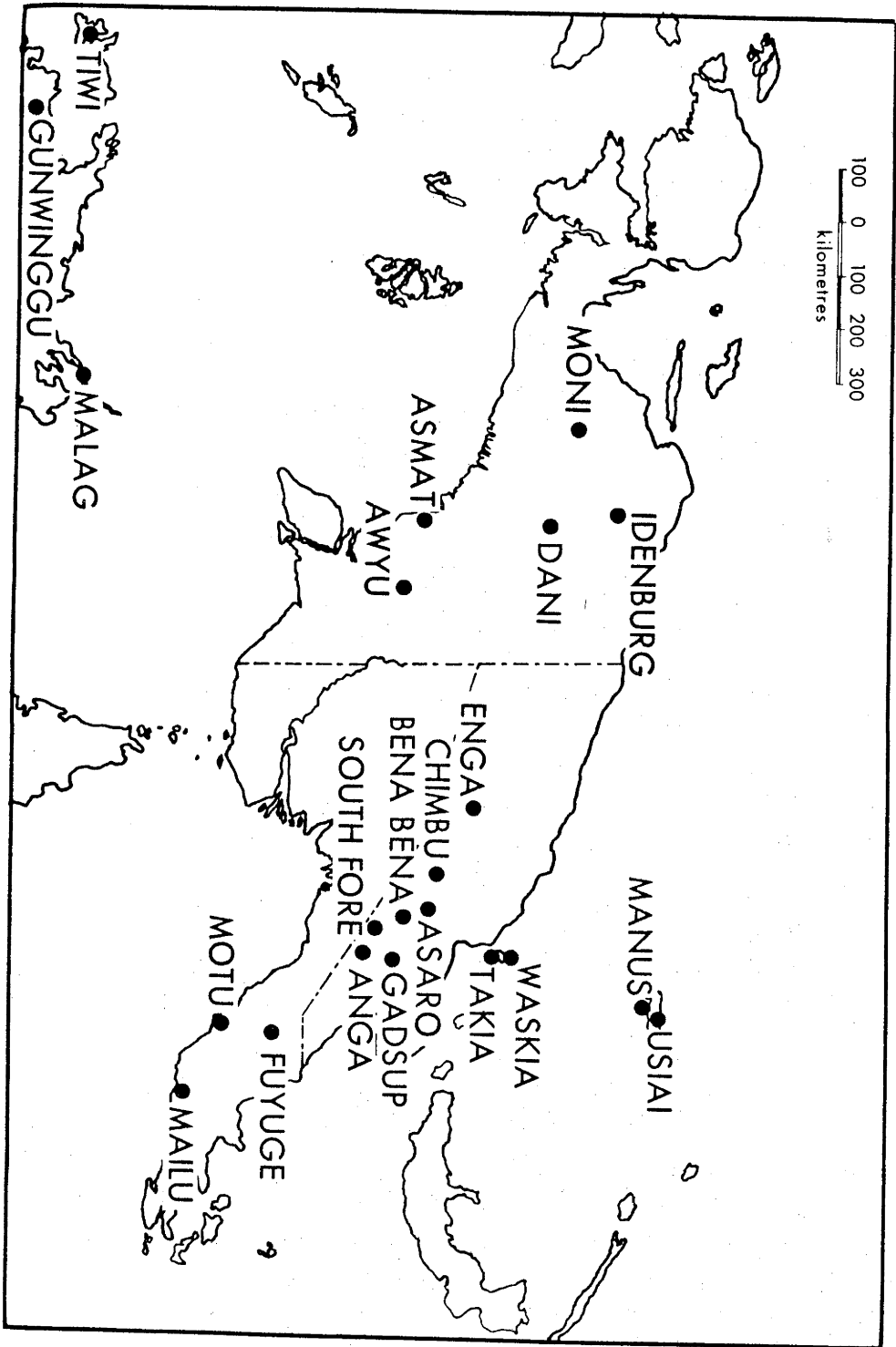
MAP 2

Map of Australia showing the areas occupied by the populations included in the study of genetic differentiation



MAP 3

Map of New Guinea showing the areas occupied by the populations included in the study of genetic differentiation



except for short periods after a heavy rain (Lawrence, 1968). The five inland populations (Aranda, Waljbiri, Bidjandjadjara, Luridja and Western Desert) live in these lowland areas.

Along the north coast of Australia the climate and vegetation are very different from that inland. The average rainfall is over 1,500 mm per annum, and cotton and rice crops are grown successfully. The two Queensland populations (Doomadgee and Mornington Island), and the populations from the north of the Northern Territory (Tiwi, Gunwinggu, Ranjbarngu, Nunggubuyu and Malag), therefore, occupy an area which is much richer in natural vegetation than that of the inland populations.

According to Capell (1971b), the Australian Aboriginal languages all show striking structural similarities to one another. However, on the basis of analysis of cognates, Wurm (1975a) has divided Australian languages into twenty-five phyletic families, of which twenty-four are located in the northern and north-western parts of the continent in one-eighth of the total area.

The Northern Territory and Western Australian populations studied speak languages which belong to four phyletic language families: Tiwian, Nunggubuyan, Gunwingguan and Pama-Nyungen; the Pama-Nyungen family is the one which is used throughout most of the continent. According to Wurm (1971b), Tiwi of the Tiwian family shares some features with the Gunwinggic group of the Gunwingguan family, of which the Ranjbarngic group is also a member. Nunggubuyu belongs to the Nunggubuyan family, while the Malag and the languages of central Australia are all classified as belonging to the Pama-Nyungen family. Within this family, Bidjandjadjara, Luridja and the Western Desert

languages belong to the same language subgroup, while Waljbiri belongs to a different subgroup of the same group. Aranda and Malag are in distinct groups of this family. The languages represented by the Mornington Island sample also belong to the Pama-Nyungen family, but those from Doomadgee have been assigned to two other phylic families (the Tangic and Karawic).

Eastern New Guinea

The island of New Guinea is divided politically into two distinct parts: Papua New Guinea and Western New Guinea. Papua New Guinea has its own Government while Western New Guinea is administered by Indonesia. The Admiralty Islands and Karkar Island are part of Papua New Guinea, while Fiji is independent.

High mountains, mostly over 4,000 metres in height, separated by broad valleys, form the backbone of the island of New Guinea. Two distinct series of mountain ranges run from east to west of the island. There are several large rivers flowing through the valleys which separate these ranges. South of the rugged central ranges the lowland becomes quite swampy. About three-quarters of the country is covered by tropical rain-forest while savannah or reed grasses grow in the drier areas (Kennedy, 1968). The rainfall is very high in New Guinea (more than 2,000 mm per annum), but its distribution is not uniform and there are distinct dry and extremely wet zones (Hart, 1970).

The highland populations used in this study live in several different regions; the Gadsup, Bena Bena, Asaro, South Fore and Anga are in the Eastern Highlands, the Chimbu in the Chimbu region, the Enga in the Western Highlands, and the Fuyuge live in the Southern Highlands. The principal crop of the highlands is the sweet potato which is well adapted to the soil and climate of this region.

Along the south-east coast of Papua New Guinea there are foothills below 600 metres leading down to small swampy areas. This region is the driest in New Guinea, having an average yearly rainfall of below 1,000 mm. The main vegetation consists of savannah and grassland, and there are few crops because of the high alkaline content of the soil (Robbins, 1970). The Motu and Mailu people who live on this coast make use of the sea for their food.

Karkar Island is situated off the coast from the Madang district of New Guinea. It has an area of approximately 320 square kilometres with the middle of the island consisting of steep broken country surrounding a volcanic crater. This part is inaccessible, but all of the villages are connected by road around the edge of the island. The main crops are coconuts and cacao, and Karkar Island probably has the most fertile land in the Territory of Papua New Guinea (IBP Human Adaptability Project in New Guinea, 1967). The north of the island is occupied by the Waskia speaking people, while the Takia speakers live in the southern part.

The Admiralty Islands (numbering about forty) lie to the north of New Guinea. The largest island is Manus which has an area of approximately 1,600 square kilometres and is mostly covered by lowland hill forest with deciduous trees and grassland in the drier parts (Haantjens, 1970). Both the Manus and Usiai linguistic groups live on this island. The Manus speaking people, who build their houses on piles over the lagoons around the coast, are relatively homogeneous. The Usiai, on the other hand, are a very mixed collection of people speaking over twenty languages (Booth and Vines, 1968).

Fiji consists of about 320 islands, only about 100 of which are inhabited. It lies approximately 3,000 kilometres east of the north-eastern coast of Australia. The principal island is Viti Levu, of which the central and south-eastern parts are covered in tropical rain forest while the remainder consists of tropical grassland, coconut palm and mangrove swamp (Kennedy, 1968).

Two radically different types of languages are spoken on the island of New Guinea; Melanesian (Austronesian) and Non-Austronesian (Papuan). Most of the Non-Austronesian languages can be allotted to large groups called phyla. These phyla can be divided into subgroups called stocks and these, in turn, into language families. The Melanesian languages have a comparatively simple structure, but the Non-Austronesian languages have a great structural complexity which is demonstrated particularly in the verbal systems (Wurm, 1970).

All of the Non-Austronesian linguistic groups used in this study belong to the Trans-New Guinea Phylum which is used in about three-quarters of the New Guinea mainland stretching from Western New Guinea to the eastern end of Papua New Guinea. Wurm (1971a, 1972) gives the following classification of these languages. Gadsup, Bena Bena, Asaro, South Fore, Chimbu and Enga belong to the East New Guinea Highlands stock, with Bena Bena, Asaro and South Fore being members of the same family. The Anga, who are geographically in the Eastern Highlands, are not classified linguistically with the other Eastern Highland groups; they belong to the Angan stock. The other Non-Austronesian languages belong to different stocks; the Fuyuge language to the Goilalan stock, the Mailu to the Mailuan stock and the Waskia (Z'graggen, 1971) to the Isumrud stock.

The Melanesian language groups of New Guinea used in this study are the Motu, Takia, Manus and Usiai. Capell (1971a) divides their languages into two groups with Manus and Usiai belonging to the first group, while Motu and Takia are in the second group. The Manus and Usiai languages show strong Micronesian influences (Booth and Vines, 1968), and the Motu language has been mixed with both Polynesian and Micronesian languages (Groves *et al.*, 1958). The Fijian language is usually classified as Melanesian, although the people and the language have Polynesian features as well (Milner, 1971).

Western New Guinea

The structure of Western New Guinea varies from extremely high mountain ranges to large swamplands, dissected by dozens of wide, interconnecting rivers. Most of these rivers are very difficult to navigate due to treacherous tides (Simmons *et al.*, 1967). About eighty percent of Western New Guinea is covered with tropical forest, containing valuable species of trees which grow to an enormous height. Along the coast mangrove trees and sago palm are found. Sago is the main item of diet in this coastal area, but inland, where the land rises toward the mountain ranges, yam, sweet potato and sugar cane are grown (Report on Netherlands New Guinea, 1960). The Moni and Dani people live in the highlands, while the people speaking languages belonging to the Idenburg-Rauffaer-Mamberamo Family live in the Central Lake Plain area which is north of the mountains. The Asmat people live in the coastal swamps and build their houses on poles or in trees. East of the Asmat, the Awyu live inland on the banks of rivers.

All of the languages spoken by the populations studied in Western New Guinea are Non-Austronesian and belong to the Trans-

New Guinea Phylum. Each of the groups represents a separate language family within that Phylum.

Population Genetic Studies in Australia and New Guinea

Population genetic studies reveal that the populations of Australia and New Guinea differ in blood genetic markers (see Kirk, 1965a for review). However, such studies have revealed that a number of specific genetic markers occur in both countries (Kirk, 1976). It is possible that the most widespread of these specific markers, the transferrin variant, D_1 , was present at the time when the countries were bound together as a single landmass (before about 8,000 B.P.). More geographically localized markers, such as Gc Aborigine or Peptidase B6, could have been introduced by independent mutation, but it is more probable that they represent introductions of new alleles from one country into the other as a result of migrations, either planned or accidental.

The analysis in this study examines the relationships among populations in Australia and New Guinea using the technique of kinship (Morton, 1973a,b, and c) calculated from gene frequencies. It is clear that the evolutionary history of man in Australia and New Guinea is very complex and it may be difficult to reconstruct this history by analysing the frequencies of genes in living populations. However, if the analysis of the data shows that two populations are more closely related genetically to one another than to a random group of individuals, it would be likely that there has been gene flow between them since the time that they originally shared a common gene pool. It is possible, of course, that by random drift alone two populations may evolve in a similar way, but this is extremely unlikely to continue for thousands of

years, especially if the groups are small. Therefore, migration has probably been the major evolutionary force contributing to the genetic similarity which this study will show exists between some populations in Australia and New Guinea.

The genetic structure of the populations discussed above was examined in terms of nine polymorphisms. These are the three blood group systems, ABO, MNS, and Rh, four red cell enzyme systems, acid phosphatase (Phs), 6-phosphogluconate dehydrogenase (6PGD), and two phosphoglucomutase loci (PGM_1 and PGM_2), and two serum protein systems, haptoglobin (Hp) and transferrin (Tf). The sources of the published data are listed in Appendix 6. Additional data were obtained from records in the Department of Human Biology at the Australian National University (data on each system were available for all populations).

For the ABO system A and O are the only groups found in most parts of Australia, although the B gene occurs in a few northern Australian populations. In New Guinea, A, B, and O are all present, with A and B having similar frequency ranges. The S antigen of the MNS system is not found in full-blood Australian Aborigines, but it is present (though often with low frequency) in most parts of New Guinea. In general, the N frequency is higher than the M in both Australia and New Guinea. R^O (cDe), R^1 (CDe), R^2 (cDE) and R^Z (CDE) of the Rh system are commonly found in Australia, but only the first three are common in New Guinea. The red cell enzyme systems show some interesting features. The B allele of acid phosphatase has a high frequency in New Guinea, and it is fixed in most Australian populations. The two common alleles, A and C of 6PGD are present in both Australia and New Guinea.

However, a third allele PGD^{Elcho} has been found in Arnhem Land, but has not so far been found elsewhere. There are two PGM loci detectable in red cells. At the first locus, two alleles, PGM₁¹ and PGM₁² occur in all populations. The PGM₁³ gene has been found in parts of New Guinea, but not in Australia, while a small frequency of the PGM₁⁶ gene was detected only at Doomadgee in Australia. The second locus was thought to be monomorphic in almost all human populations. However, recently two alleles, PGM₂⁹ and PGM₂¹⁰, were found to be widely distributed in New Guinea but absent from Australia. On the other hand, another allele, PGM₂³, has been found in central Australian populations but not in northern Australia or New Guinea (Blake and Omoto, 1975). The two serum proteins also show some distinctive variation. In Australia the Hp¹ gene frequency is always less than 0.5 with the Hp² gene having frequencies above 0.5. In New Guinea, however, the reverse is true; the frequency of Hp¹ is greater than 0.5 and that of Hp² is below 0.5. The D₁ allele of transferrin is widespread in Australia and New Guinea; another transferrin variant, D_{Manus} is found only on Manus Island (Malcolm *et al.*, 1972). Reviews of variation in gene frequencies in Australia and New Guinea are given by Simmons (1976) for blood groups and by Kirk (1976) for red cell enzymes and serum proteins.

Chapter 8

GENETIC DIFFERENTIATION: RESULTS FOR POPULATIONS WITHIN
AUSTRALIA AND NEW GUINEA

Four sets of populations were chosen for the kinship analysis. These consisted of: (1) the twelve Australian populations, (2) the fifteen linguistic groups from Eastern New Guinea (3) the five populations representing language families in Western New Guinea, and (4) the fifteen Non-Austronesian speaking groups from Eastern and Western New Guinea. In this chapter these sets of populations are analysed separately. In the next chapter the populations of Australia are compared with those of New Guinea.

Australia

The kinship matrix for the Australian populations is shown in Table 16. The highest kinship values are within and between the two Queensland populations, Doomadgee (Doom.) and Mornington Island (M.I.), which implies that they have been fairly isolated from the rest of the populations, and also provides genetic evidence that movement has taken place between these two groups in recent times. The kinship results also suggest that the Mornington Island group is related to four of the northern populations, Tiwi, Gunwinggu (Gun.), Ranjbarngu (Ranj.) and Nunggubuyu (Nung.). This may have been due to an outside influence which added new genes to each of these populations, rather than migration between Arnhem Land and the bottom of the Gulf of Carpentaria. The Western Desert (W.D.) population is closest genetically to the Luridja (Lurid.) and Bidjandjadjara (Bid.) groups (which is in agreement with linguistic relationships). The four central Australian

TABLE 16

Kinship between Australian Populations

	Doom.	M.I.	W.D.	Aranda	Walj.	Lurid.	Bid.	Malag	Nung.	Ranj.	Gun.	Tiwi
Doom.	.0676											
M.I.	.0480	.1001										
W.D.	-.0298	-.0493	.0349									
Aranda	.0017	.0002	-.0082	.0178								
Walj.	-.0114	.0052	-.0059	.0091	.0454							
Lurid.	-.0192	-.0286	.0127	.0081	.0192	.0225						
Bid.	-.0216	-.0363	.0165	.0073	.0015	.0166	.0373					
Malag	-.0081	-.0150	.0039	-.0031	-.0134	-.0026	.0065	.0150				
Nung.	-.0121	.0067	-.0083	-.0069	-.0048	-.0116	-.0063	.0101	.0403			
Ranj.	-.0070	.0123	-.0138	-.0019	-.0037	-.0068	-.0110	.0104	.0139	.0320		
Gun.	.0152	.0277	-.0195	-.0048	-.0064	-.0150	-.0148	.0057	.0132	.0172	.0214	
Tiwi	.0174	.0284	-.0172	-.0079	-.0184	-.0233	-.0342	-.0035	.0073	.0108	.0118	.0672

populations (Luridja, Bidjandjadjara, Aranda and Waljbiri (Walj.)) are all genetically related to one another. Linguistic evidence and Peterson's (1976) drainage basins hypothesis suggest that the Aranda have not mixed with the Waljbiri, Luridja or Bidjandjadjara. The genetic analysis, however, suggests that movement has occurred among all four of these linguistic groups. Movement between the Aranda and both Queensland populations, and the Waljbiri and Mornington Island populations is also suggested. The kinship within these groups indicates that the movement has been mainly from the north to the south. The Malag are related linguistically to the central populations, and they show some genetic relationship to the Bidjandjadjara and the Western Desert groups. However, they are genetically closer to the northern populations (Nunggubuyu, Ranjbarngu and Gunwinggu) which are all related. The high kinship within the Tiwi who live on Bathurst Island, suggests that they have been quite isolated, and that their relationship with the northern mainland populations (Nunggubuyu, Ranjbarngu and Gunwinggu) is due to movement from rather than to the island. The eigenvector representation (Figure 9a) and the dendrogram (Figure 9b) show the main features of the kinship matrix; the cophenetic correlations (R) indicate that the eigenvector representation conserves more information than the dendrogram.

A recent publication by Balakrishnan *et al.* (1975) which gives a detailed analysis of genetic distances between Australian populations using the B statistic of Balakrishnan and Sanghvi (1968), and adds to the analyses of Sanghvi *et al.* (1971) and Kirk *et al.* (1972b) gives results consistent with those of this study. These authors used slightly different sets of populations and loci from those used in the present analysis, but the

FIGURE 9a

Eigenvector Representation of Kinship Matrix for Australian Populations

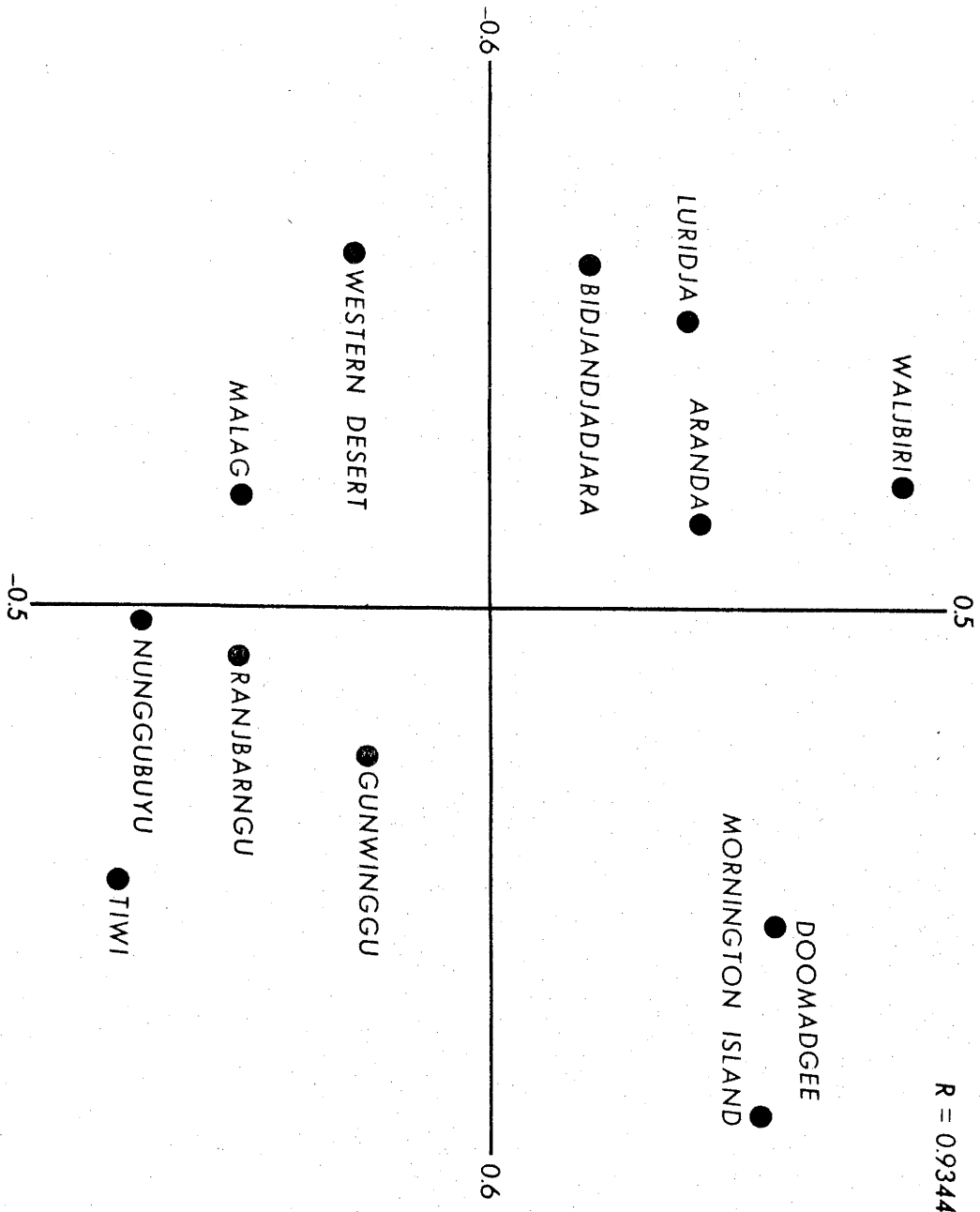
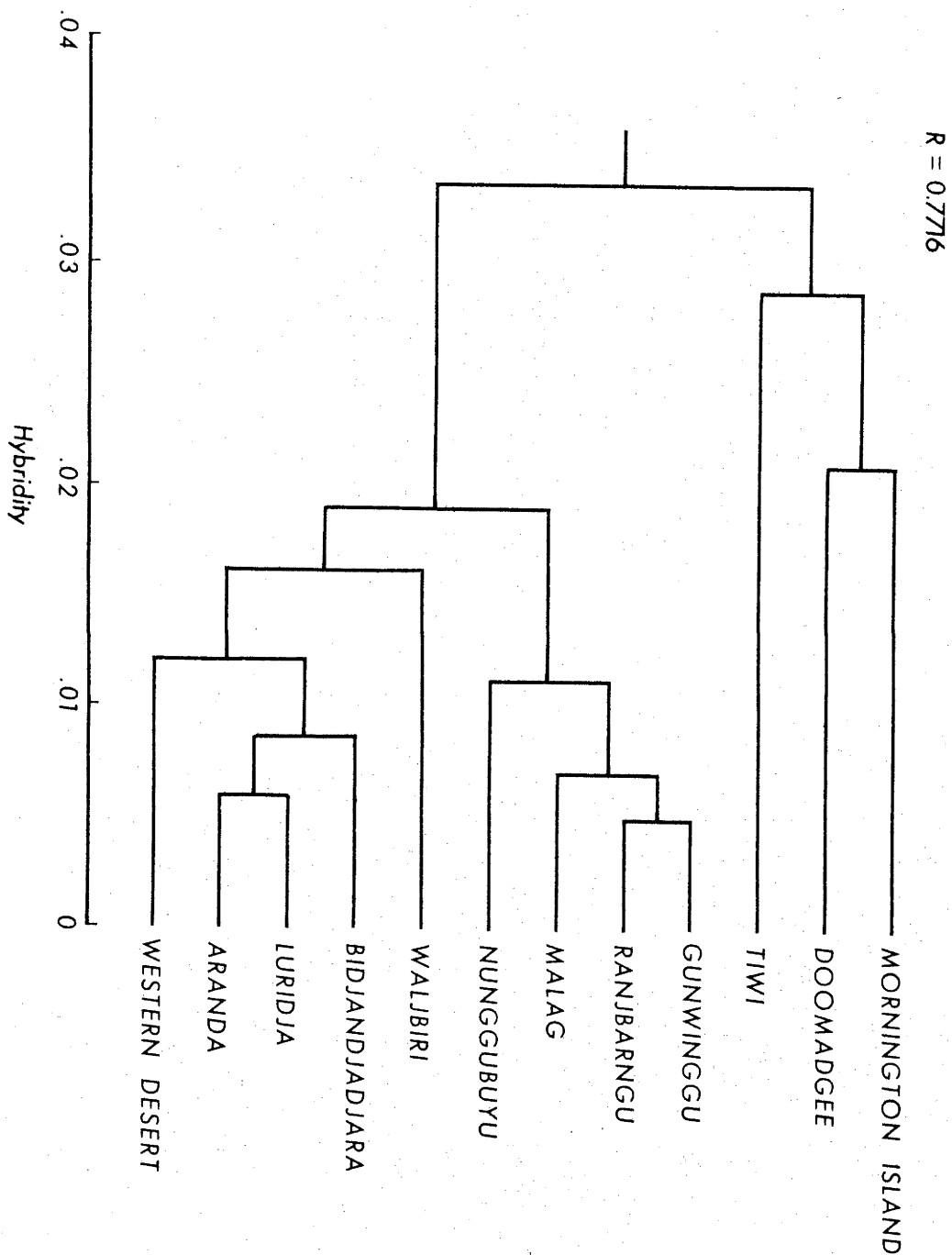


FIGURE 9b

Dendrogram from Kinship Matrix for Australian Populations



picture of genetic diversity that they obtained is similar. Other analyses of Australian populations were carried out by Kirk (1973) who calculated genetic distances between populations at localities in Cape York, the Northern Territory and Western Australia, and Parsons and White (1973) who used data on four central and four northern Australian populations and found a positive correlation between distance statistics based on gene frequencies and those based on dermatoglyphics.

The loci chosen for a genetic distance analysis are assumed to represent a random sample from the genome, and, in general, some are more variable than others. In the present analysis the regional homozygosity was found to be highest for acid phosphatase (Phs) (.9835) because the Phs^B gene is either close to or is fixed in all of the populations studied, while Rh had the lowest value (.4736) since there are four alleles found in most of the Australian populations. The largest mean kinship was obtained for MNS (.1082) indicating that this system shows the most variation between populations. Acid phosphatase (Phs) has the smallest mean kinship (.0068) and is exceeded (in order) by 6PGD, PGM₂, Hp, Tf, Rh, PGM₁, ABO and MNS (Table 17).

The mean kinship as a function of geographic distance for the Australian populations was calculated by dividing the distances between populations into subsets. Equation 6.20 was then fitted to these data. Figure 10 shows the mean kinship values plotted against the midpoint of the geographic distance class, and the line of best fit through these points. The parameter values obtained were:

$$\begin{array}{ll} a = .0568 & \sigma_a = .0083 \\ b = .0024 & \sigma_b = .0012 \\ L = -.0139 & \sigma_L = .0070 \end{array}$$

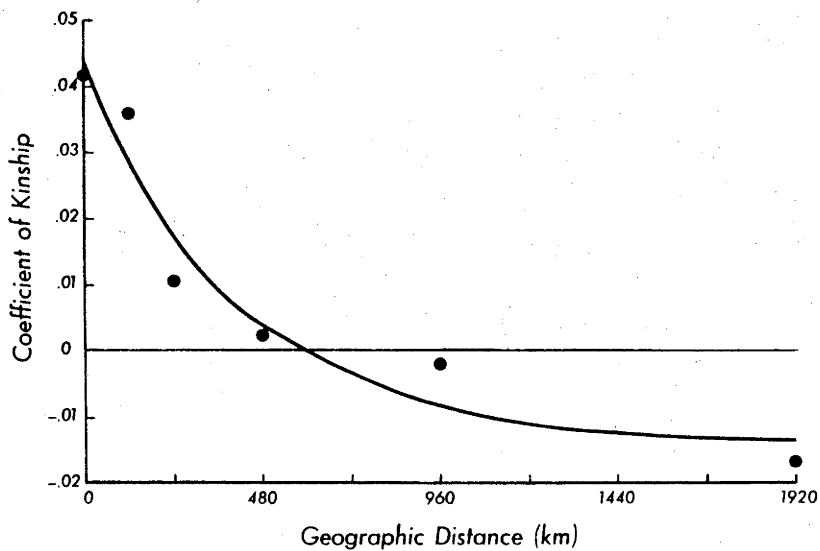
TABLE 17

Regional Homozygosity and Mean Kinship
within Australian Populations

System	Regional Homozygosity	Mean Kinship
ABO	.6105	.0565
MNS	.6479	.1082
Rh	.4736	.0495
Phs	.9835	.0068
6PGD	.8945	.0227
PGM ₁	.7702	.0496
PGM ₂	.9749	.0265
Hp	.6359	.0300
Tf	.7668	.0343

FIGURE 10

Plot of Kinship against Geographic Distance
and the line of best fit of Equation 6.20 to
these data for the Australian Populations



The local kinship parameter (a) is quite high but the decline of kinship with distance (b) is slow. Both of these parameter values are very similar to those obtained by Morton and Lalouel (1973) for Micronesia. The values suggest that the genetic relationships of the Australian populations may fit Berndt's (1959) hypothesis that local groups travelled large distances and often came into contact with one another for the purposes of trade which sometimes included exchange of people from each group.

Eastern New Guinea

The results of the analysis of the populations from Eastern New Guinea, are shown in the kinship matrix (Table 18). The kinship within the Fijians is very high indicating their isolation from most of the other populations. The kinship for the Usiai group from the Admiralty Islands also suggests isolation of that group. However, the high kinship between the Manus and the Usiai, who live on the same island, indicates that movement has occurred between these two groups. The Usiai and Fijian groups also have a high kinship between them, and it is interesting to note that the populations to which the Fijians are related are the four other Melanesian groups (Motu, Takia, Manus and Usiai), and the coastal population Mailu (which linguistically is Non-Austronesian, but which may have been influenced by the surrounding Melanesian populations). However, the high kinship within the Mailu, suggests that this influence was not from populations used in the present analysis. The five Melanesian populations are all related to one another. The low kinship within and between the Waskia (Non-Austronesian) and the Takia suggests that there has been migration into and out of these groups, but not between them despite the fact

TABLE 18

Kinship between Eastern New Guinea Populations

	Gadsup	Bena	Asaro	Sth. Fore	Chimbu	Enga	Anga	Fuyuge	Waskia	Mailu	Motu	Takia	Manus	Usiai	Fiji
Gadsup	.0172														
Bena	.0023	.0107													
Asaro	.0063	.0122	.0259												
Sth.Fore	.0046	.0056	.0061	.0143											
Chimbu	.0009	.0053	.0117	.0086	.0295										
Enga	.0050	.0016	.0041	.0002	.0132	.0370									
Anga	.0150	.0085	.0134	.0029	.0100	.0112	.1031								
Fuyuge	.0000	.0001	.0032	.0050	.0019	.0017	.0067	.0161							
Waskia	.0025	.0037	.0020	.0032	.0068	.0055	.0098	.0009	.0172						
Mailu	.0099	.0007	.0116	.0127	.0017	.0033	.0046	.0095	.0026	.0927					
Motu	.0016	.0038	.0012	.0148	.0143	.0210	.0048	.0006	.0020	.0005	.0334				
Takia	.0071	.0041	.0088	.0089	.0140	.0110	.0040	.0021	.0029	.0013	.0095	.0112			
Manus	.0027	.0017	.0064	.0203	.0151	.0217	.0242	.0074	.0057	.0134	.0176	.0051	.0721		
Usiai	.0045	.0046	.0196	.0195	.0173	.0191	.0318	.0092	.0123	.0285	.0094	.0033	.0828	.1273	
Fiji	.0162	.0069	.0213	.0070	.0172	.0300	.0017	.0050	.0137	.0283	.0165	.0123	.0322	.0635	.0949

that they share the same island. This lack of movement between these two linguistic groups is also seen in the migration analysis carried out by Harrison *et al.* (1974). The Waskia are, however, genetically related to some of the highland (Non-Austronesian) groups, and there are indications of relationships between some other highland, and coastal and island populations. The Fuyuge, for example, are closer genetically to some of the coastal and island groups than to other highland populations. The high kinship within the Anga group suggests that there has been very little migration either into or out of that group; it is not closely related to any of the other linguistic groups used in this study. The remaining six highland groups (Gadsup, Bena Bena, Asaro, South Fore, Chimbu and Enga) are all related to one another, and the Chimbu and Enga are also related to the Waskia. A summary of the kinship matrix is provided by the eigenvector representation (Figure 11a) and the dendrogram (Figure 11b).

The genetic clustering of these populations does not show the distinct separation which occurs when they are divided into two groups by language type. However, the conclusion reached by Booth and Taylor (1976), that the clustering of the populations corresponds reasonably well with the major linguistic division, is supported.

The regional homozogysity and mean kinship at each locus (Table 19) differ from those found for the Australian populations. The highest mean homozygosity is for transferrin (Tf) (.9228) whereas for the Australian populations the value for transferrin is .7668. The value for PGM₂ is high in both sets of populations. The lowest value for Eastern New Guinea is for ABO (.5202) compared with a value of .6105 found in

FIGURE 11a
Eigenvector Representation of Kinship Matrix for
Eastern New Guinea Populations

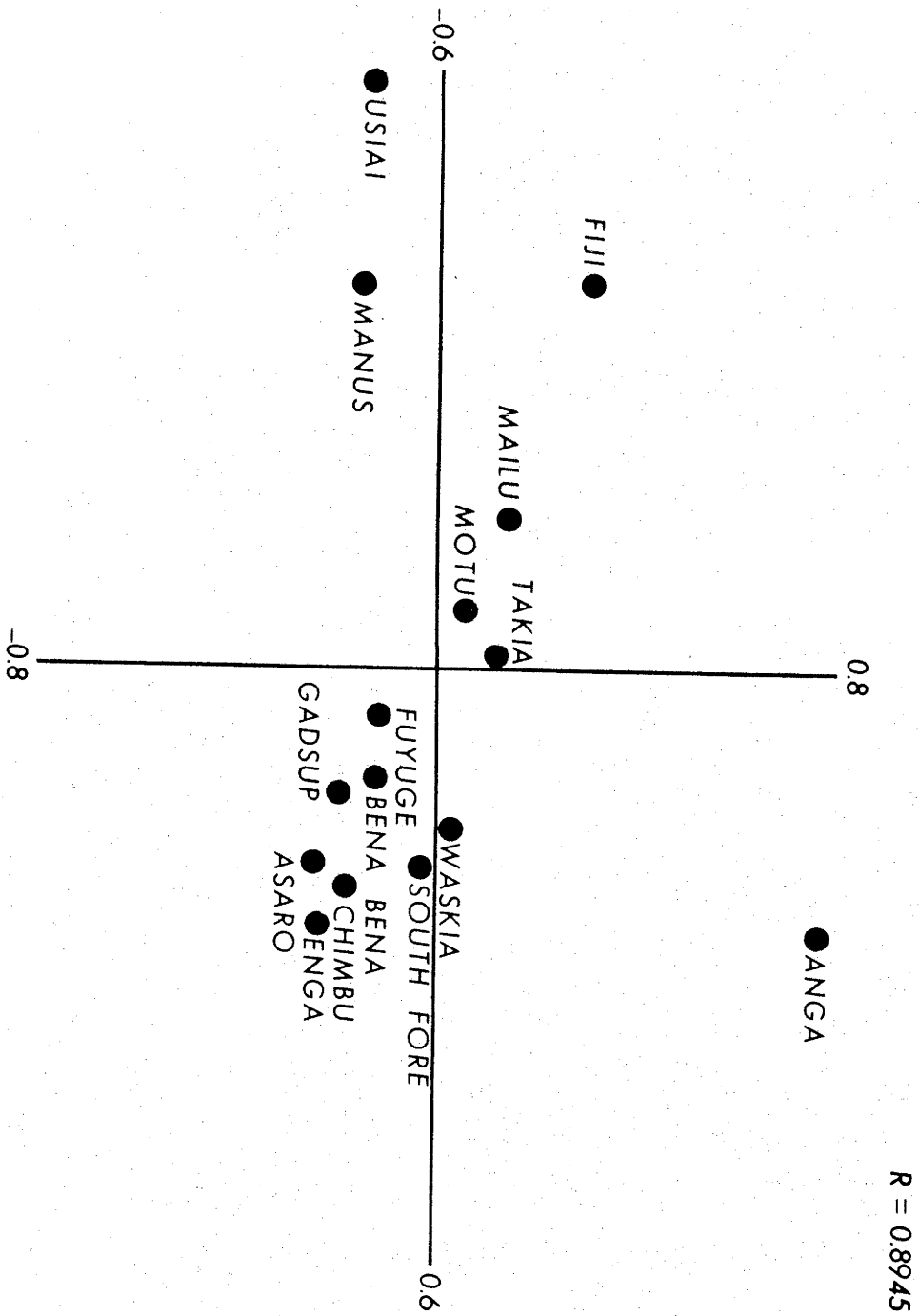
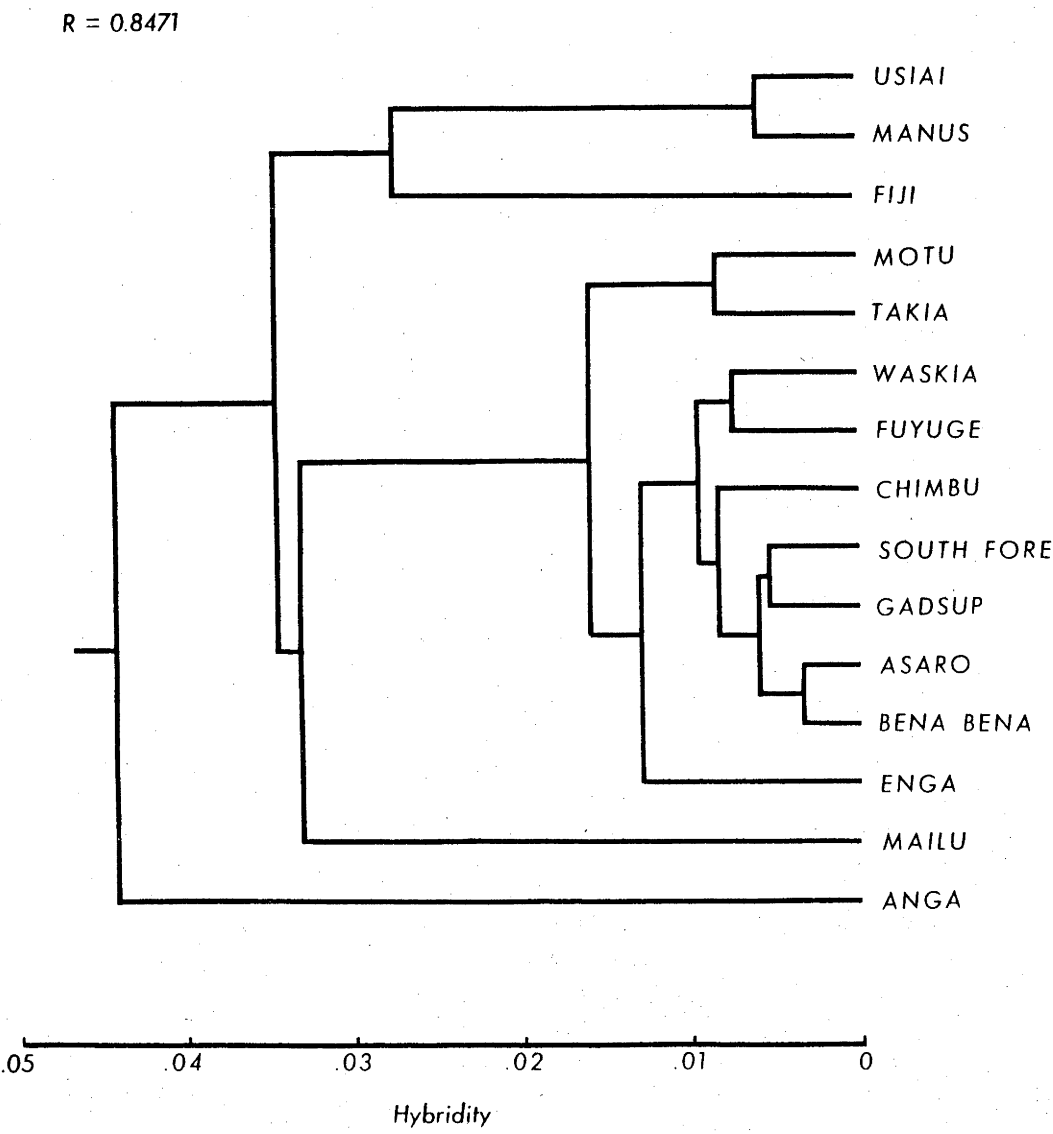


FIGURE 11b

Dendrogram from Kinship Matrix for Eastern New
Guinea Populations



Australia. Rh, on the other hand, which gave the smallest value for the Australian populations, is quite high for Eastern New Guinea because the frequency of the R^1 allele is above 0.8 for all of the Eastern New Guinea populations. The largest mean kinship in Eastern New Guinea is for MNS (.0781) as it is in Australia, indicating that this system shows the most variation among populations in both countries. In Eastern New Guinea the lowest mean kinship is for transferrin (.0190). ABO, PGM_2 , Rh, 6PGD, Phs, Hp, PGM_1 , MNS (in that order), exceed the transferrin value. The greatest difference between the Eastern New Guinea and Australian populations is for acid phosphatase, with the New Guinea populations having more than four times the mean kinship value found for those in Australia. The values for 6PGD, PGM_1 , PGM_2 , and Hp, on the other hand, are very similar in both countries.

Figure 12 shows that mean kinship in Eastern New Guinea does not decrease monotonically with increasing geographic distance. This indicates that kinship often corresponds more closely with linguistic similarity than with geographic proximity. The line of best fit of Equation 6.20 gave parameter values of

$$\begin{array}{ll} a = .0344 & \sigma_a = .0050 \\ b = .0494 & \sigma_b = .0179 \\ L = -.0001 & \sigma_L = .0021 \end{array}$$

The estimates of a and b describe the genetic structure of New Guinea with local kinship being quite high (although significantly lower than that in Australia), and the decrease with distance much more rapid than that found for Australia. Neither a nor b are significantly different from the values obtained by Imaizumi and Morton (1970) using data from four

TABLE 19

Regional Homozygosity and Mean Kinship
within Eastern New Guinea Populations

System	Regional Homozygosity	Mean Kinship
ABO	.5202	.0217
MNS	.6363	.0781
Rh	.8165	.0253
Phs	.7023	.0294
6PGD	.8362	.0259
PGM ₁	.8621	.0465
PGM ₂	.8694	.0238
Hp	.5492	.0393
Tf	.9228	.0190

FIGURE 12

Plot of Kinship against Geographic Distance and the
line of best fit of Equation 6.20 to these data for
the Eastern New Guinea Populations

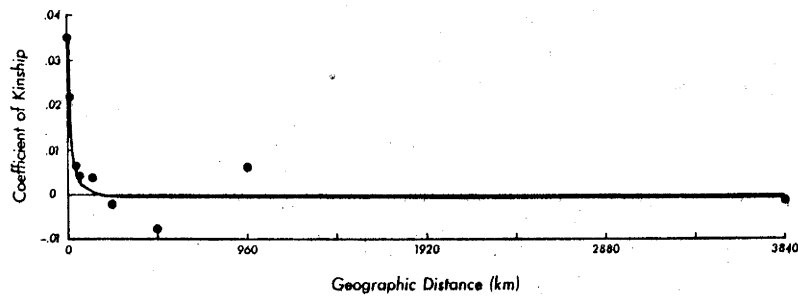


TABLE 20

Kinship between Western New Guinea Populations

	Asmat	Awyu	Moni	Idenburg	Dani
Asmat	.0059				
Awyu	-.0056	.0563			
Moni	-.0010	-.0229	.0289		
Idenburg	-.0030	-.0284	.0074	.0431	
Dani	.0032	-.0223	.0014	.0005	.0214

isolated areas of New Guinea, but both values are significantly lower than those obtained by Friedlaender (1971) for Bougainville. Therefore, although migrational distances are much shorter in Australia, movement is not as restricted in Eastern New Guinea as it is in Bougainville.

Western New Guinea

Table 20 shows the kinship matrix for the five populations from Western New Guinea. The "within population" kinship value is highest for the Awyu which is not closely related genetically to any of the other four populations. The Asmat are close to the Dani but not to the Moni or Idenburg people. This suggests movement between the Dani and the Asmat, which may have been made possible by travelling along the Baliem River, which flows from the central highlands to the Asmat coast. The three northern populations (Moni, Idenburg and Dani) are genetically related to one another. The relationships among these five groups are summarized in the eigenvector representation (Figure 13a) and the dendrogram (Figure 13b).

The regional homozygosity and mean kinship within the Western New Guinea populations (Table 21) are similar to the values for Eastern New Guinea. The highest regional homozygosity

FIGURE 13a
 Eigenvector Representation of Kinship Matrix for
 Western New Guinea Populations

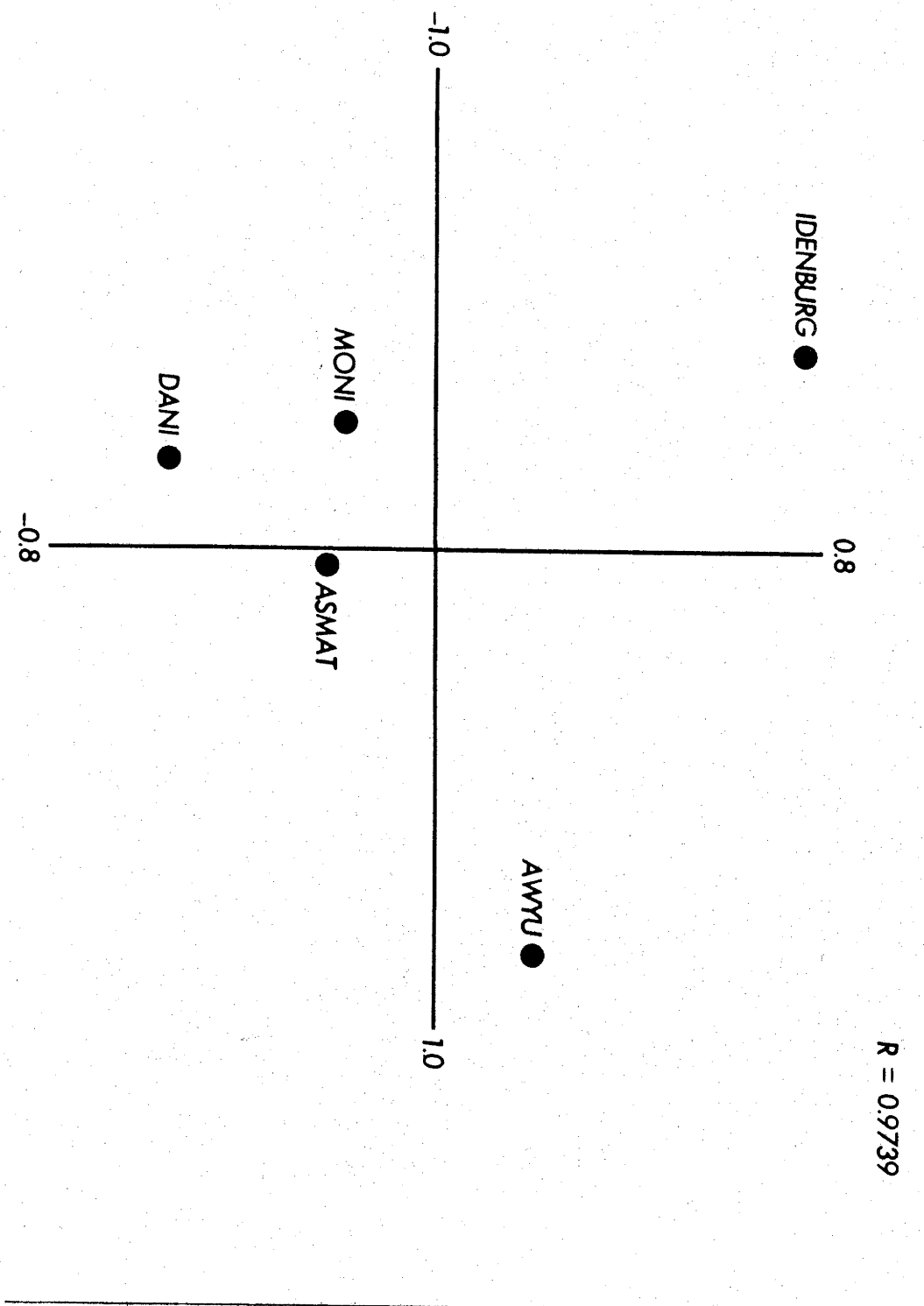


FIGURE 13b

Dendrogram from Kinship Matrix for Western New Guinea Populations

$R = 0.8923$

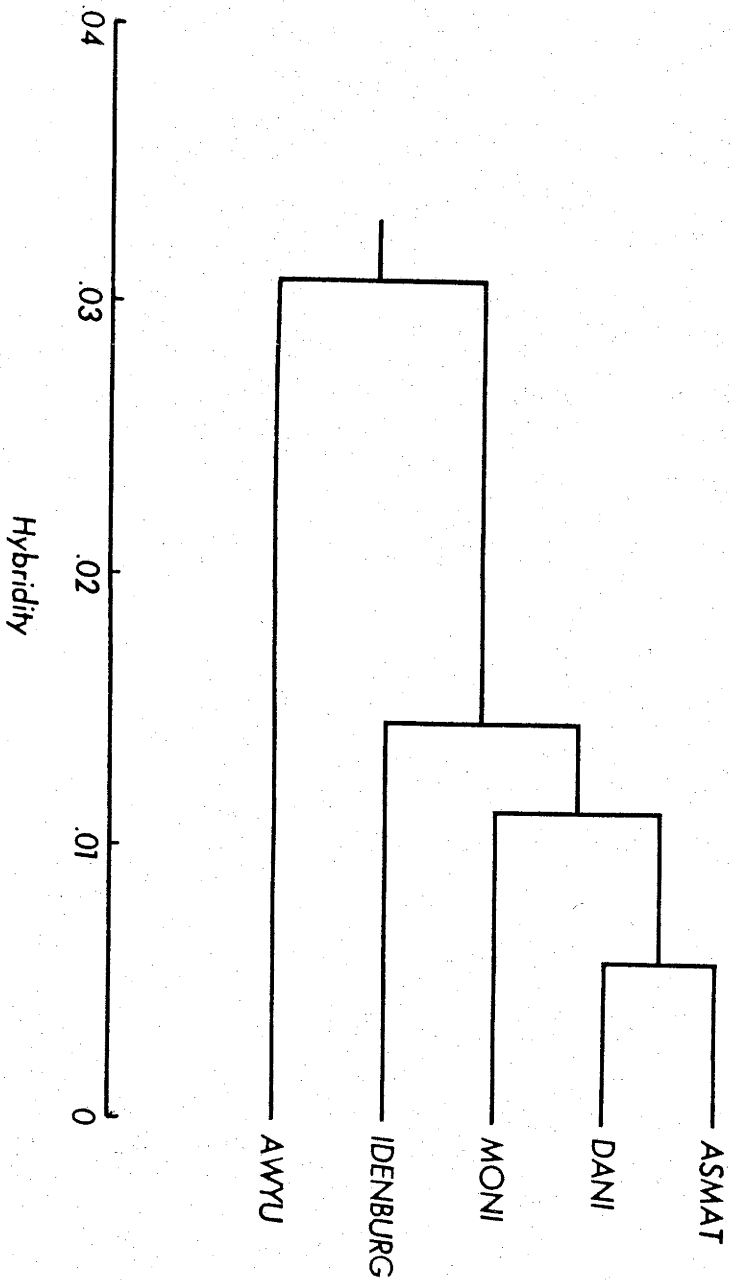


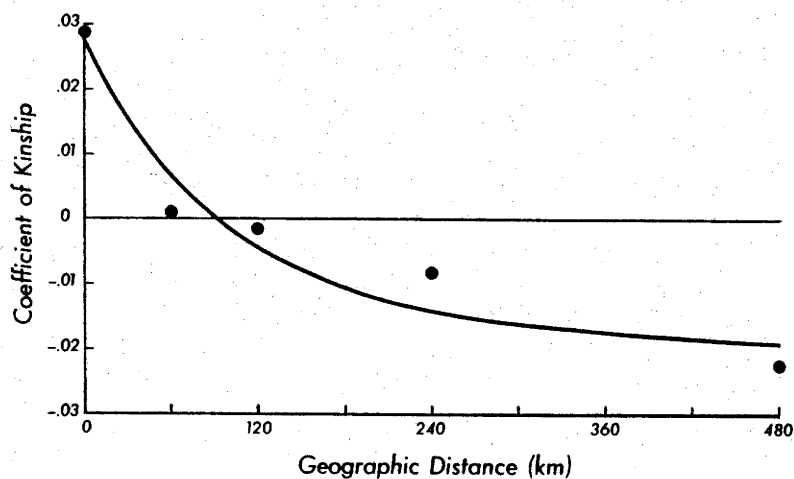
TABLE 21

Regional Homozygosity and Mean Kinship
within Western New Guinea Populations

System	Regional Homozygosity	Mean Kinship
ABO	.4728	.0234
MNS	.6660	.0467
Rh	.8624	.0254
Phs	.6291	.0184
6PGD	.7040	.0224
PGM ₁	.8358	.0467
PGM ₂	.7963	.0165
Hp	.6693	.0457
Tf	.8630	.0282

FIGURE 14

Plot of Kinship against Geographic Distance and the
line of best fit of Equation 6.20 to these data for
the Western New Guinea Populations



is for transferrin (.8630) and the lowest is for ABO (.4728); the positions of these two systems are the same as were found for Eastern New Guinea, although the values for Western New Guinea have a smaller magnitude.

In the case of mean kinship the highest value is for MNS (.0467), as it was for both Eastern New Guinea and Australia, but the value is much lower than for those two sets of populations. The value for PGM_1 is the same as that for MNS. The smallest mean kinship is for PGM_2 (.0165) and the values for each system increase in the order Phs, 6PGD, ABO, Rh, Tf, Hp to MNS and PGM_1 .

Kinship decreases with geographic distance in Western New Guinea (Figure 14) and the line of best fit of equation 6.20 has parameter values of

$$\begin{array}{ll} a = .0452 & \sigma_a = .0093 \\ b = .0092 & \sigma_b = .0047 \\ L = -.0193 & \sigma_L = .0076 \end{array}$$

The local kinship (a) is about the same as that found for Eastern New Guinea, but the decrease with distance occurs much more slowly, although it is significantly faster than in Australia. This indicates that migration in Western New Guinea has been over longer distances than in Eastern New Guinea, which suggests, perhaps, that it is easier to move from one area to another in Western New Guinea than in the other half of the island.

Non-Austronesians

Non-Austronesian speaking populations are found in both Eastern New Guinea and Western New Guinea; 15 have been included in this study. The kinship values between these populations are shown in Table 22. The highest values are found

TABLE 22

Kinship between Non-Austronesian Speaking Populations in New Guinea

	Gadsup	Bena	Asaro	Sth. Fore	Chimbu	Enga	Anga	Fuyuge	Waskia	Mailu	Asmat	Awyu	Moni	Idenburg	Dani
Gadsup	.0168														
Bena	.0053	.0168													
Asaro	.0092	.0161	.0264												
Sth. Fore	.0015	.0069	.0047	.0117											
Chimbu	-.0039	.0033	.0068	.0021	.0166										
Enga	-.0017	-.0012	.0000	-.0053	.0030	.0227									
Anga	-.0014	.0122	.0045	.0100	.0013	-.0060	.0691								
Fuyuge	.0030	.0058	.0066	-.0032	-.0017	-.0035	.0068	.0184							
Waskia	.0024	.0067	.0072	-.0021	.0093	.0036	.0183	.0105	.0286						
Mailu	-.0030	.0089	-.0031	-.0080	-.0012	-.0029	.0199	.0008	.0107	.0942					
Asmat	-.0023	-.0048	-.0082	-.0058	-.0037	-.0074	-.0130	-.0003	-.0061	.0007	.0132				
Awyu	-.0251	-.0177	-.0167	-.0189	-.0053	.0133	-.0256	-.0063	-.0145	-.0106	.0040	.0829			
Moni	.0144	.0042	.0086	.0030	-.0059	.0015	.0099	-.0007	-.0040	-.0019	-.0053	-.0197	.0234		
Idenburg	.0118	.0037	.0117	-.0050	.0014	-.0083	-.0052	.0072	.0116	.0050	-.0017	-.0242	-.0022	.0458	
Dani	.0051	-.0129	-.0133	-.0024	-.0040	-.0123	-.0177	-.0058	-.0136	-.0148	.0113	-.0124	.0016	.0093	.0363

within the Anga, Mailu and Awyu, which indicates that these populations have been isolated from the other groups. The four Eastern Highland populations are genetically related to one another and also to the Moni group in the highlands of Western New Guinea. However, the other Western New Guinea highland population, the Dani, is closest genetically to the coastal Western New Guinea group, the Asmat.

Each Non-Austronesian population is genetically related to at least two other populations from this group. The relationships between them are shown in the eigenvector representation and the dendrogram in Figures 15a and 15b, respectively.

As would be expected, the regional homozygosity and mean kinship at each locus are similar to those for the Eastern and Western New Guinea sets of populations. The highest regional homozygosity is for transferrin (.8884) and the lowest is for ABO (.4868); this is true for each of the three sets of populations. MNS again has the largest mean kinship value (.0582), so that for all four of the population sets described in this chapter, the greatest variability among populations is found for the MNS blood group system. The smallest mean kinship is for PGM_2 (.0163), and this value is exceeded (in order) by Rh, Phs, Tf, ABO, 6PGD, Hp, PGM_1 and MNS (Table 23).

The decline of kinship with geographic distance for the Non-Austronesian populations (Figure 16) is similar to that found when all the New Guinea groups are included in the analysis. That is, kinship does not decrease monotonically as distance increases indicating that groups separated by large distances are more closely related genetically than some groups separated by short distances. The fit of equation 6.20 to these data gave parameter values of

FIGURE 15a
Eigenvector Representation of Kinship Matrix for Non-Austronesian
Speaking Populations

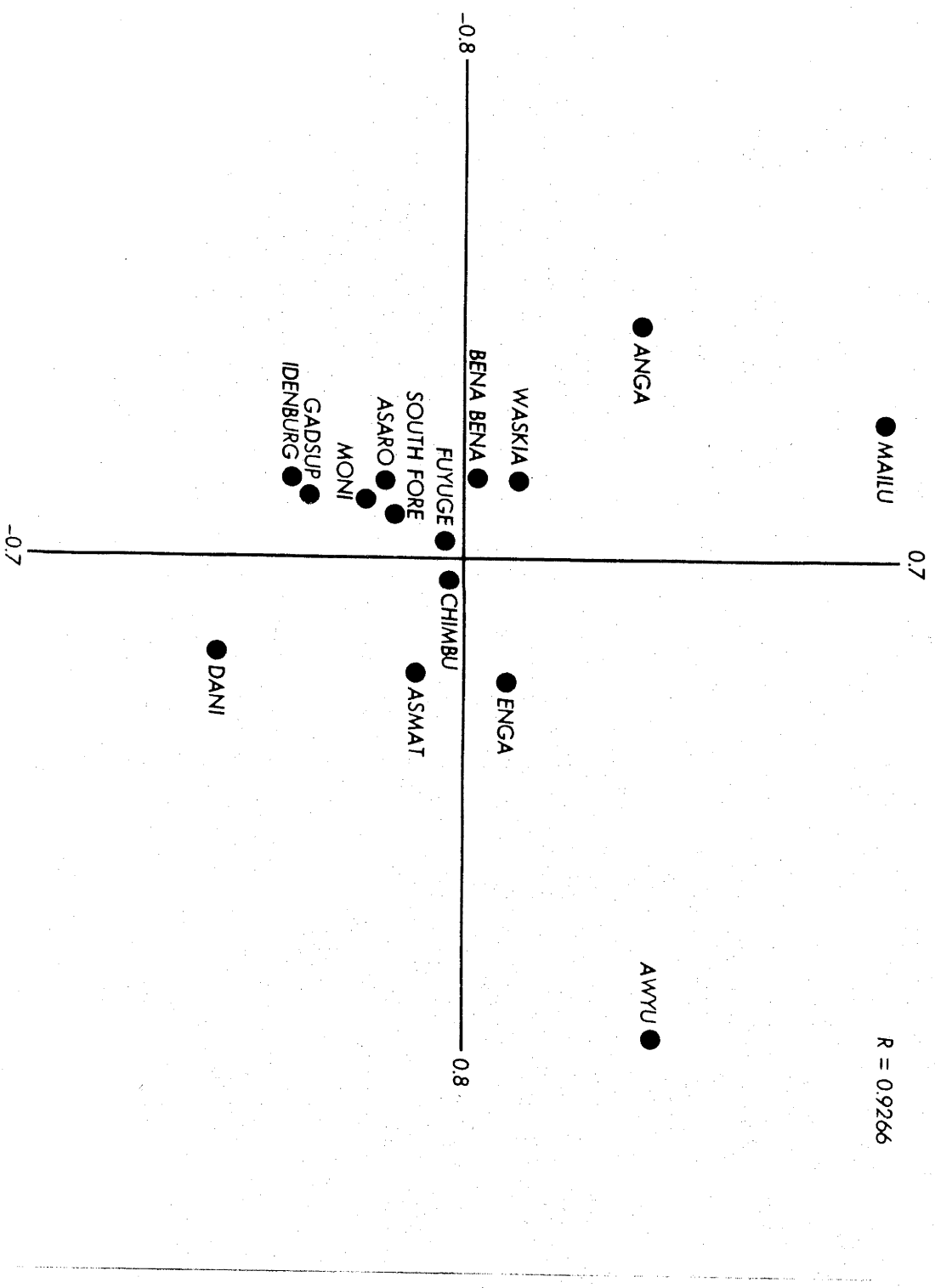


FIGURE 15b

Dendrogram from Kinship Matrix for Non-Austronesian
Speaking Populations

$R = 0.8841$

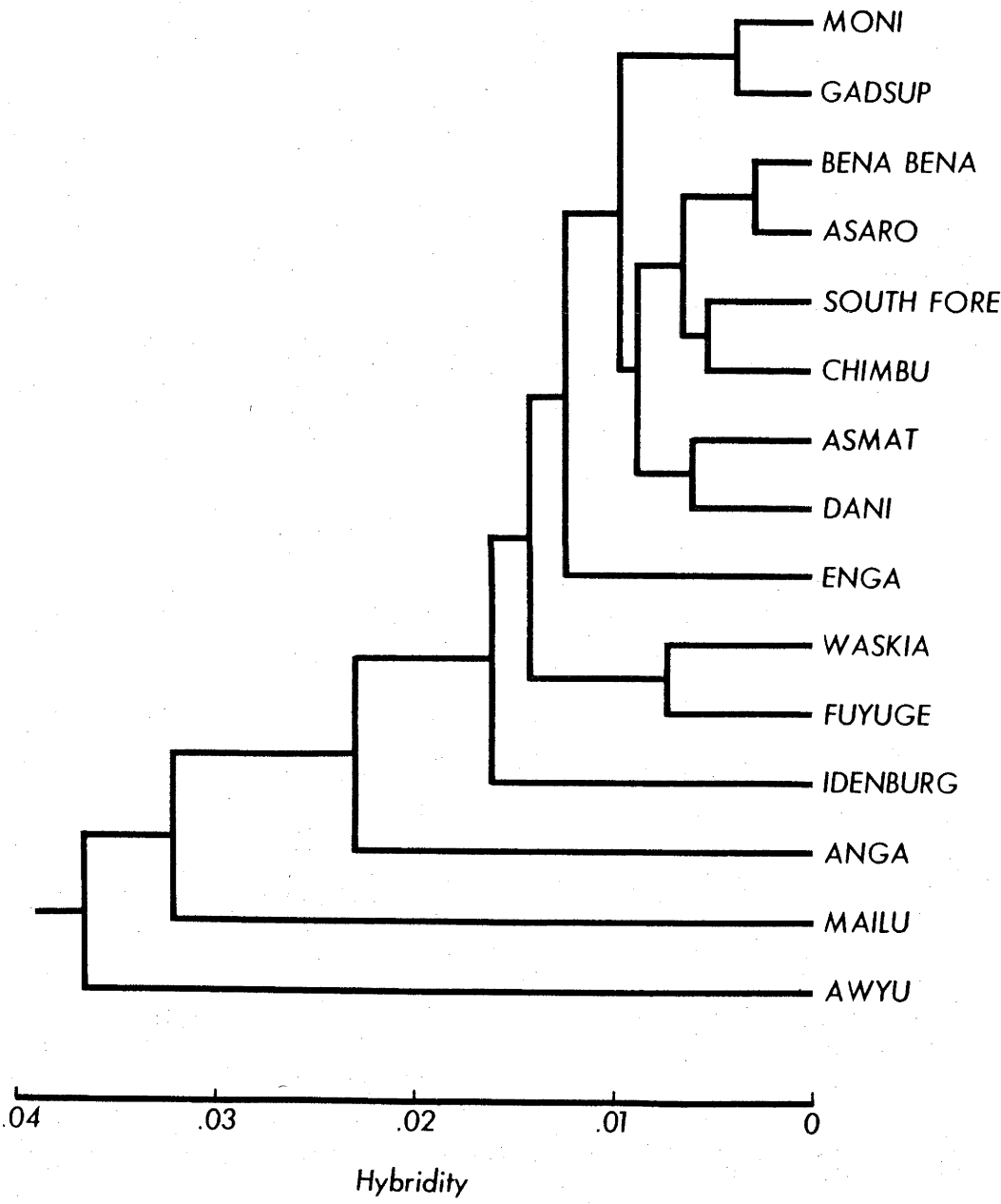


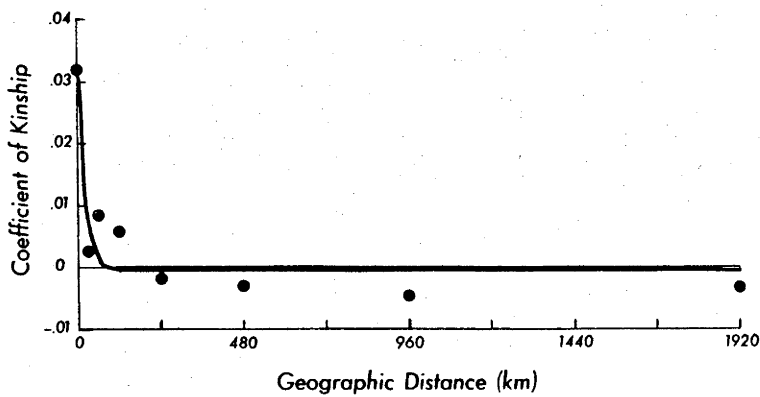
TABLE 23

Regional Homozygosity and Mean Kinship
within Non-Austronesian Populations

System	Regional Homozygosity	Mean Kinship
ABO	.4868	.0262
MNS	.6982	.0582
Rh	.8439	.0192
Phs	.6392	.0238
6PGD	.7602	.0397
PGM ₁	.8597	.0420
PGM ₂	.8046	.0163
Hp	.6162	.0397
Tf	.8884	.0254

FIGURE 16

Plot of Kinship against Geographic Distance and
the line of best fit of Equation 6.20 to these
data for the Non-Austronesian Populations



$$\begin{array}{ll} a = .0313 & \sigma_a = .0057 \\ b = .0530 & \sigma_b = .0255 \\ L = -.0006 & \sigma_L = .0023 \end{array}$$

The local kinship (a) is not significantly different from the values obtained for the Eastern and Western New Guinea populations. The rate of decrease of kinship with distance is about the same as that in Eastern New Guinea, but is significantly higher than in Western New Guinea. It appears that movement between Non-Austronesian populations in New Guinea is very restricted even between those which are close geographically. However, the changes in gene frequencies within these populations due to genetic drift and selection appear to be either small or similar for each population, because even those separated by large distances, between whom movement is very unlikely to have occurred, are often related genetically.

Chapter 9

GENETIC DIFFERENTIATION: RESULTS BETWEEN
AUSTRALIAN AND NEW GUINEA POPULATIONS

The populations of Australia and New Guinea may be combined to obtain kinship values among populations in both countries, and also among populations within each country relative to the larger regional population.

Australia and Eastern New Guinea

Table 24 shows the kinship between populations in Australia and Eastern New Guinea. Although most of the values are negative (suggesting that the populations are not closely related), two Melanesian groups (Motu and Fiji) are related to the Queensland groups, Doomadgee and Mornington Island. The Motu also show some resemblance to the Ranjbarngu of Australia, and the Manus Islanders are genetically related to the Tiwi. This suggests that the outside influence which seems to have affected the northern Australian populations may have been due to Melanesians from New Guinea coming to the northern coast of Australia. Booth and Taylor (1976), using only blood group data for a few Northern Territory and coastal Papuan populations, have also found a relatively short genetic distance between the Motu and northern Australian populations. The eigenvector representation (Figure 17a) and the dendrogram (Figure 17b) summarize the kinship matrix and suggest that the Melanesian populations are genetically close to those in Northern Australia.

The regional homozygosity for the combined populations falls between that for Australia and that for Eastern New Guinea

TABLE 24

Kinship between Australian and Eastern New Guinea Populations

	Doom.	M.I.	W.D.	Aranda	Walj.	Lurid.	Bid.	Malag	Nung.	Ranj.	Gun.	Tiwi
Gadsup	-.0438	-.0438	-.0505	-.0465	-.0536	-.0560	-.0643	-.0434	-.0407	-.0306	-.0369	-.0238
Bena	-.0383	-.0416	-.0336	-.0348	-.0416	-.0396	-.0449	-.0430	-.0399	-.0384	-.0416	-.0200
Asaro	-.0413	-.0433	-.0418	-.0411	-.0526	-.0463	-.0470	-.0435	-.0412	-.0335	-.0430	-.0185
Sth.Fore	-.0323	-.0487	-.0263	-.0324	-.0442	-.0288	-.0366	-.0288	-.0392	-.0214	-.0279	-.0276
Chimbu	-.0564	-.0670	-.0529	-.0540	-.0644	-.0565	-.0593	-.0607	-.0624	-.0547	-.0601	-.0512
Enga	-.0776	-.0673	-.0752	-.0722	-.0736	-.0802	-.0929	-.0786	-.0643	-.0596	-.0671	-.0505
Anga	-.0243	-.0237	-.0111	-.0129	-.0141	-.0111	-.0182	-.0261	-.0235	-.0213	-.0253	-.0135
Fuyuge	-.0287	-.0276	-.0528	-.0365	-.0470	-.0517	-.0584	-.0406	-.0378	-.0330	-.0329	-.0172
Waskia	-.0432	-.0476	-.0542	-.0407	-.0536	-.0510	-.0547	-.0498	-.0534	-.0431	-.0466	-.0385
Mailu	-.0387	-.0330	-.0391	-.0297	-.0240	-.0326	-.0343	-.0486	-.0399	-.0360	-.0330	-.0355
Motu	.0020	.0099	-.0219	-.0013	-.0071	-.0118	-.0131	-.0057	-.0050	.0018	-.0012	-.0035
Takia	-.0215	-.0102	-.0386	-.0222	-.0261	-.0363	-.0433	-.0390	-.0321	-.0334	-.0318	-.0113
Manus	-.0043	-.0022	-.0569	-.0273	-.0373	-.0466	-.0580	-.0398	-.0381	-.0284	-.0221	.0047
Usiai	-.0040	-.0001	-.0656	-.0371	-.0392	-.0569	-.0757	-.0543	-.0458	-.0408	-.0261	-.0019
Fiji	.0145	.0251	-.0249	-.0086	-.0060	-.0184	-.0274	-.0278	-.0239	-.0244	-.0092	-.0122

FIGURE 17a

Eigenvector Representation of Kinship Matrix for Australia and Eastern New Guinea Populations

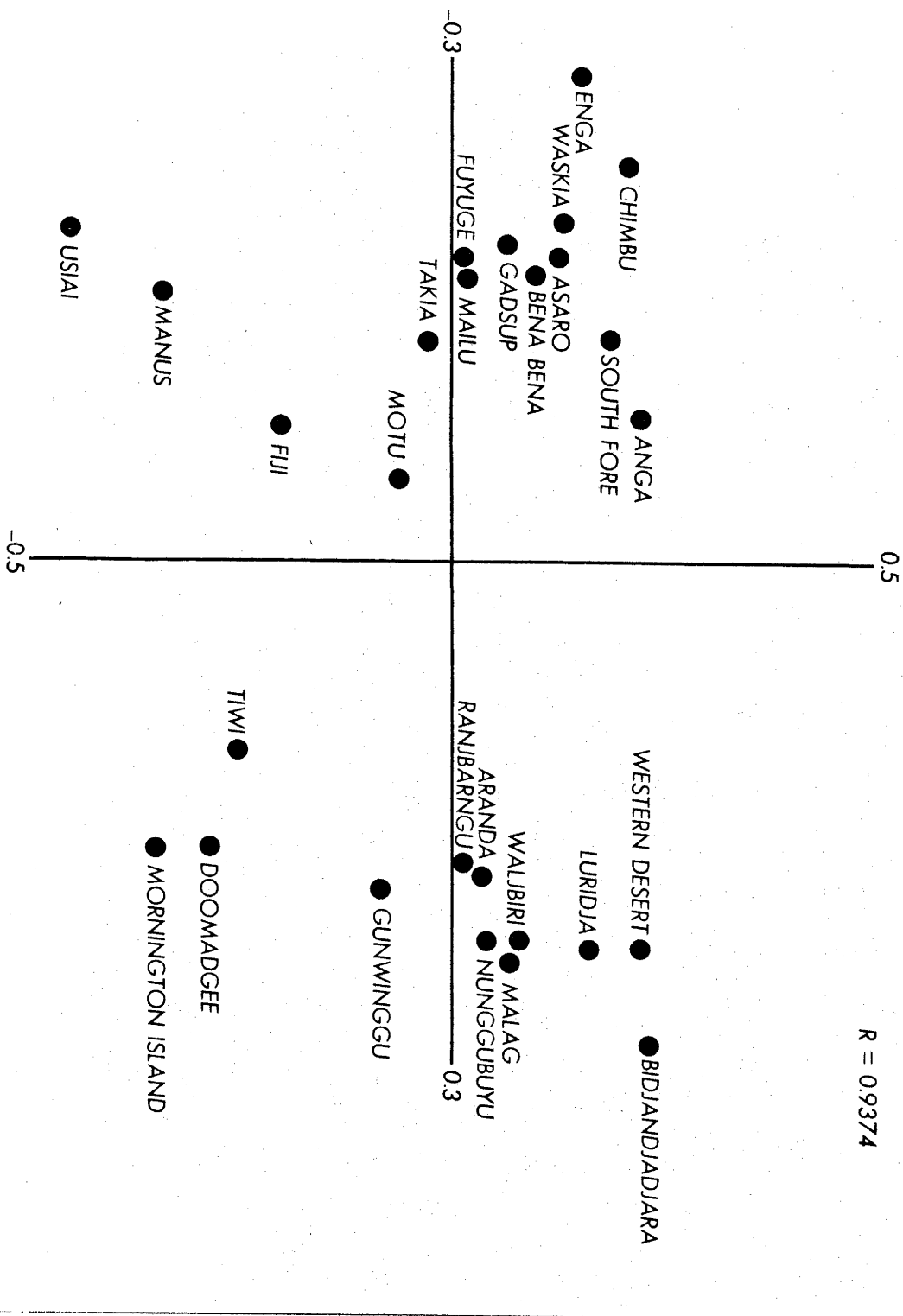


FIGURE 17b

Dendrogram from Kinship Matrix for Australian and
Eastern New Guinea Populations

$R = 0.8344$

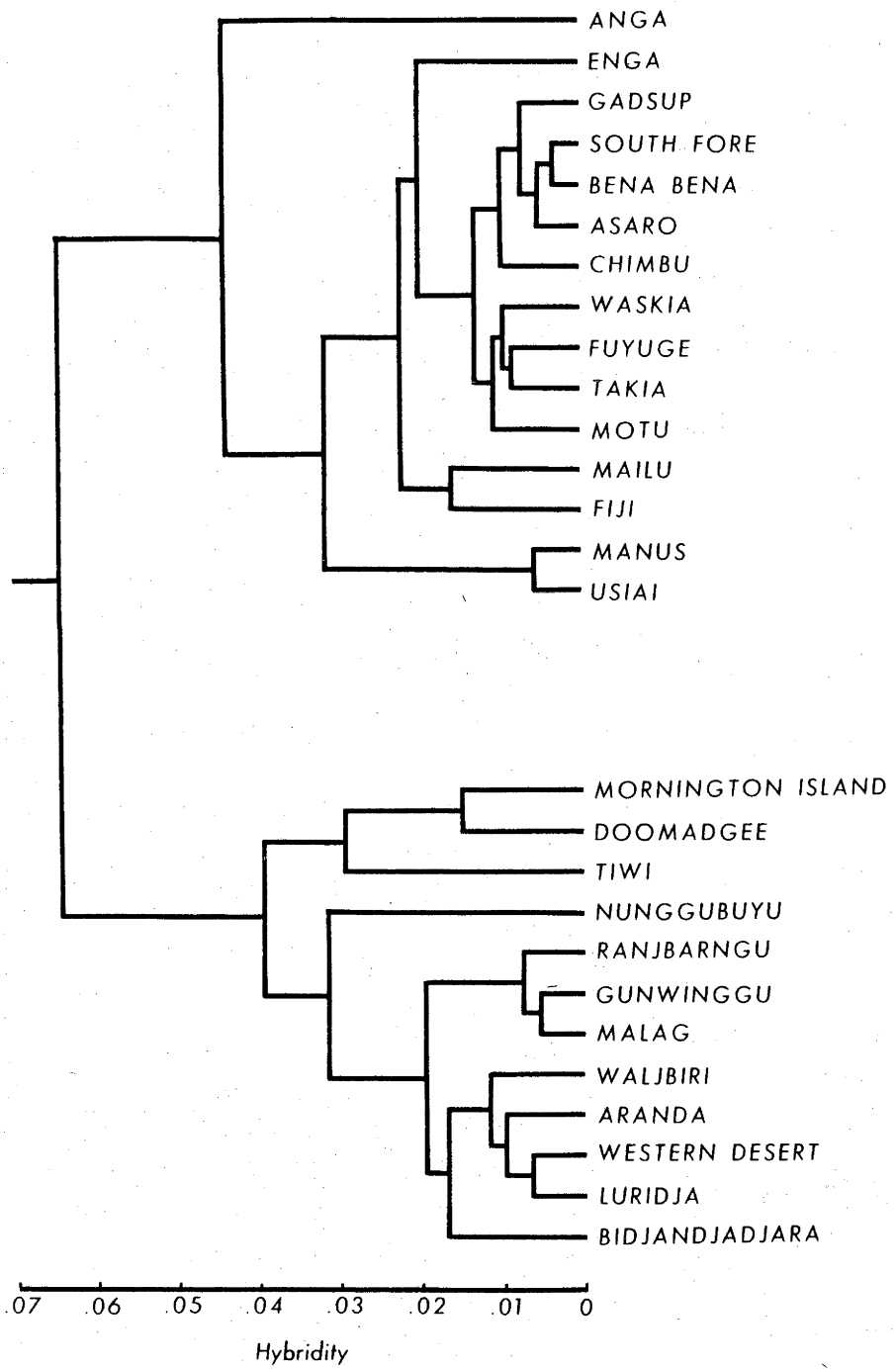


TABLE 25

Regional Homozygosity and Mean Kinship within
Australian and Eastern New Guinea Populations

System	Regional Homozygosity	Mean Kinship
ABO	.5442	.0444
MNS	.6358	.0894
Rh	.6834	.0747
Phs	.7972	.0972
6PGD	.8582	.0275
PGM ₁	.8245	.0493
PGM ₂	.9090	.0362
Hp	.5001	.1962
Tf	.8597	.0381

for most systems (Table 25), as would be expected when the gene frequencies cover the same range of values in both countries. However, in the case of haptoglobin, the Hp¹ frequency is always above 0.5 in New Guinea, and always below 0.5 in Australia, while the reverse is true for the Hp² allele. Therefore, the combined regional homozygosity is lower than that in either country considered separately. PGM₂ (.9090) has the highest regional homozygosity, while the lowest value is for Hp (.5001). For mean kinship the values for the combined populations are generally higher than when they are considered separately. This is because the variation within the countries tends to be less than that between them. The highest mean kinship is for haptoglobin (.1962) (Table 25); this is much higher than the values found for Australia (.0300) and for Eastern New Guinea (.0393). A similar situation is seen for Rh and acid phosphatase, since for each of these

systems the variation within the countries is much less than that between them. On the other hand, the kinship values within the combined populations for MNS (.0894) and PGM_1 (.0493) are very similar to those found for each country when they are considered separately, because the variation within each country is as great as that between them. The smallest mean kinship is for 6PGD (.0275) and the values increase in the order PGM_2 , Tf, ABO, PGM_1 , Rh, MNS, Phs and Hp. For ABO, MNS, and PGM_1 , the mean kinship for the region is larger than that within Eastern New Guinea but smaller than that within Australia because for these systems the Australian populations show more variation among themselves than between themselves and the New Guinea populations.

Australia and Western New Guinea

None of the populations of Western New Guinea show any close genetic relationship to the Australian populations since all of the kinship values are highly negative (Table 26). This would be expected because all of the Western New Guinea populations are Non-Austronesian speakers, and, therefore, it is consistent with the relationships found between Australian and Eastern New Guinea populations where only Melanesian speaking groups were found to be genetically related to Australian populations. Figures 18a and 18b show the eigenvector representation and the dendrogram respectively, for the Australian and Western New Guinea populations.

As in the previous section, the regional homozygosity values for the combined populations are between those determined for the two sets considered separately, with haptoglobin being an exception (Table 27). Again, the highest regional homozygosity is for PGM_2 (.8734) and the lowest is for Hp

TABLE 26

Kinship between Australian and Western New
Guinea Populations

	Asmat	Awyu	Moni	Idenburg	Dani
Doom.	-.0445	-.0660	-.0495	-.0359	-.0504
M.I.	-.0532	-.0547	-.0361	-.0376	-.0572
W.D.	-.0558	-.0916	-.0468	-.0671	-.0690
Aranda	-.0442	-.0859	-.0443	-.0329	-.0554
Walj.	-.0531	-.0897	-.0456	-.0471	-.0637
Lurid.	-.0506	-.1002	-.0549	-.0514	-.0677
Bid.	-.0589	-.1065	-.0668	-.0593	-.0827
Malag	-.0503	-.0925	-.0490	-.0518	-.0615
Nung.	-.0507	-.0796	-.0352	-.0494	-.0577
Ranj.	-.0401	-.0858	-.0345	-.0364	-.0471
Gun.	-.0420	-.0767	-.0415	-.0404	-.0482
Tiwi	-.0322	-.0528	-.0094	-.0309	-.0365

TABLE 27

Regional Homozygosity and Mean Kinship within
Australian and Western New Guinea Populations

System	Regional Homozygosity	Mean Kinship
ABO	.5346	.0968
MNS	.6500	.0896
Rh	.6113	.0865
Phs	.7512	.1268
6PGD	.7823	.0423
PGM ₁	.8035	.0507
PGM ₂	.8734	.0397
Hp	.5063	.3128
Tf	.8008	.0411

FIGURE 18a

Eigenvector Representation of Kinship Matrix for
Australian and Western New Guinea Populations

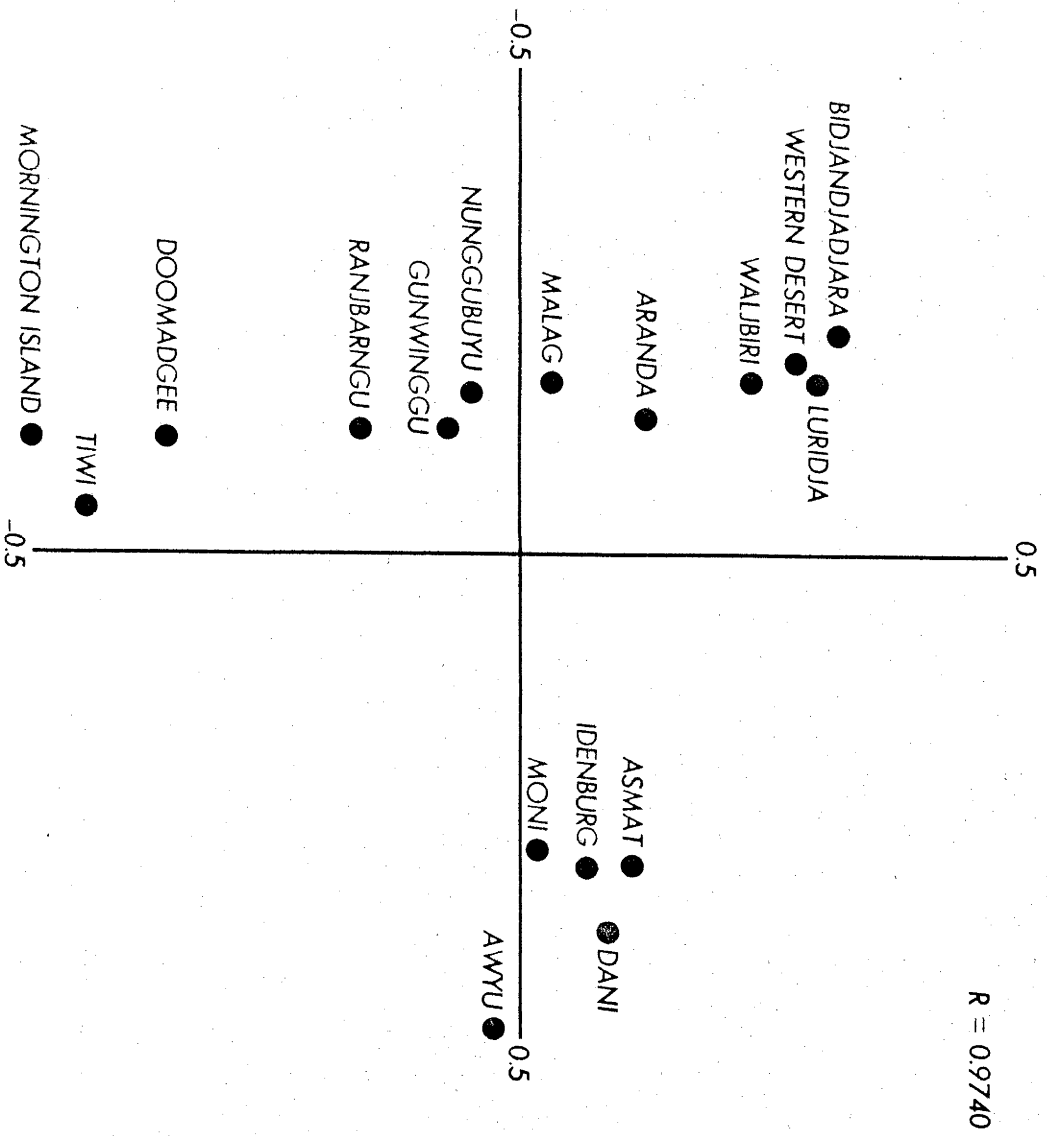
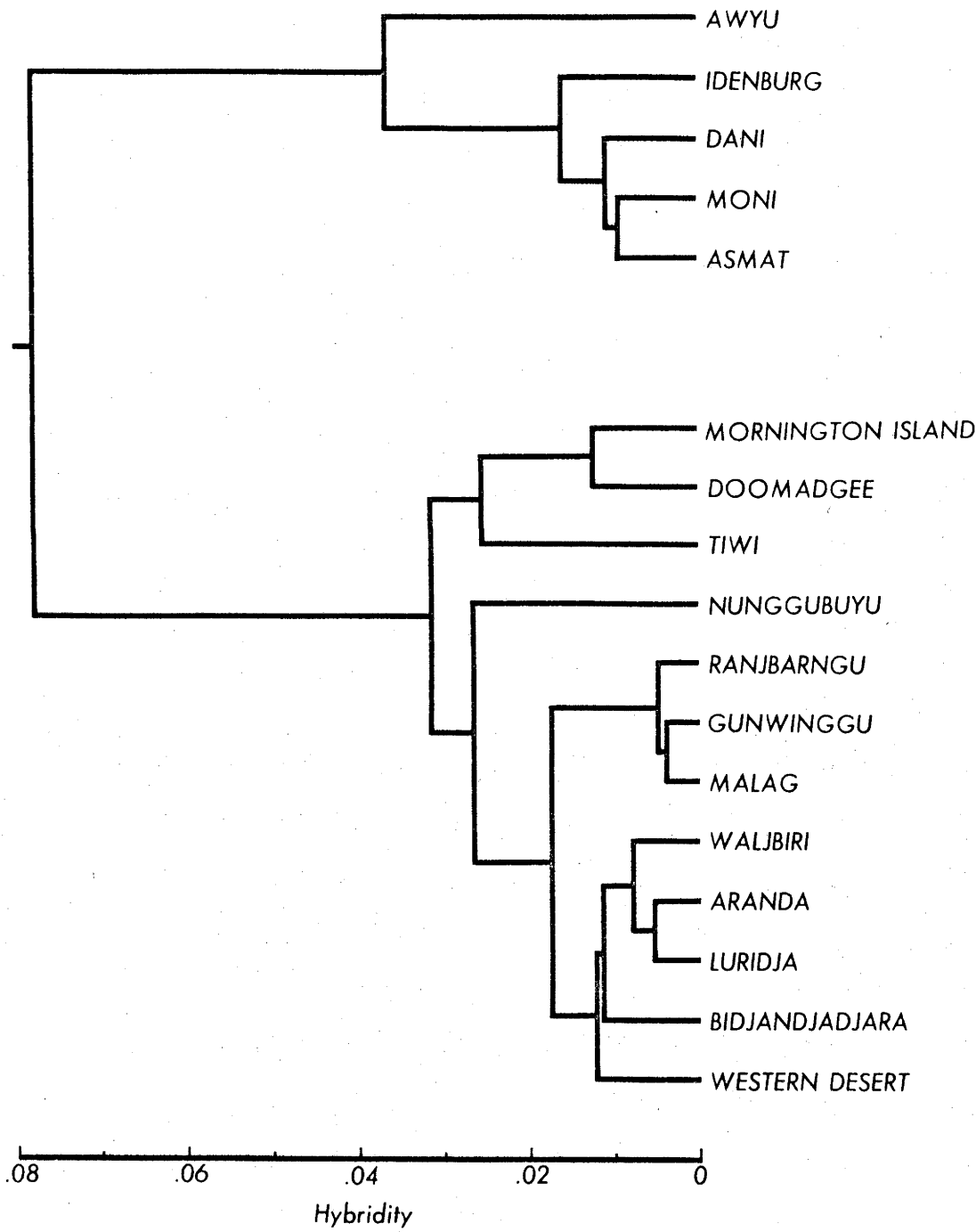


FIGURE 18b

Dendrogram from Kinship Matrix for Australian and
Western New Guinea Populations

$R = 0.8847$



(.5063). Except for MNS, the mean kinship values are all higher for the combined populations than when either country is considered separately. The highest mean kinship (.3128 for haptoglobin) is much larger than the values found for either Australia (.0300) or Western New Guinea (.0457), which indicates the differences in haptoglobin gene frequencies for these two countries. Similar differences are seen for acid phosphatase and to a lesser extent for Rh. The MNS system is much more variable in Australia than in Western New Guinea, and the mean kinship value for the two countries combined (.0896) lies between that for the two considered separately (.1082 for Australia and .0467 for Western New Guinea). For the combined populations the lowest mean kinship is obtained for PGM₂ (.0397) with the order of increase of mean kinship being Tf, 6PGD, PGM₁, Rh, MNS, ABO, Phs and Hp.

Eastern New Guinea and Western New Guinea

Both Non-Austronesian and Melanesian populations from Eastern New Guinea are genetically related to populations in Western New Guinea (Table 28). Most of the kinship values between the three northern Western New Guinea populations (Moni, Idenburg and Dani) and the highland linguistic groups of Eastern New Guinea are positive. The Idenburg population is also genetically related to the Waskia, Motu and Manus groups, but the Moni and Dani are not genetically close to any of the Melanesian populations. The coastal Western New Guinea group, the Asmat, have a positive kinship value only with the Non-Austronesian Chimbu people and the Melanesians from Manus Island. The remaining Western New Guinea group, the

TABLE 28

Kinship between Eastern New Guinea
and Western New Guinea Populations

	Asmat	Awyu	Moni	Idenburg	Dani
Gadsup	-.0017	-.0197	.0109	.0075	.0072
Bena	-.0044	-.0118	.0028	-.0014	-.0108
Asaro	-.0067	-.0086	.0061	.0091	-.0111
Sth.Fore	-.0034	-.0119	.0037	-.0054	.0021
Chimbu	.0016	.0049	-.0028	.0006	.0035
Enga	-.0006	.0206	.0058	-.0064	-.0041
Anga	-.0142	-.0192	.0078	-.0177	-.0174
Fuyuge	-.0006	-.0023	-.0020	.0003	-.0044
Waskia	-.0060	-.0094	-.0040	.0018	-.0116
Mailu	-.0011	-.0082	-.0037	-.0092	-.0166
Motu	-.0180	-.0350	-.0027	.0085	-.0235
Takia	-.0159	-.0272	-.0003	-.0008	-.0209
Manus	.0027	-.0127	-.0081	.0030	-.0122
Usiai	.0122	.0067	-.0160	-.0023	.0001
Fiji	-.0126	.0058	-.0255	-.0136	-.0203

TABLE 29

Regional Homozygosity and Mean Kinship within Eastern
New Guinea and Western New Guinea Populations

System	Regional Homozygosity	Mean Kinship
ABO	.5054	.0310
MNS	.6450	.0698
Rh	.8286	.0232
Phs	.6662	.0297
6PGD	.7748	.0413
PGM ₁	.8504	.0450
PGM ₂	.8371	.0235
Hp	.5750	.0569
Tf	.9066	.0228

Awyu, are genetically related to the Chimbu and Enga in the highlands and the Usiai on Manus Island, and the Awyu have the only positive kinship with Fiji. The Mailu and Takia linguistic groups are not genetically related to any of the Western New Guinea populations. The clustering of the Moni and the Idenburg with the Eastern Highland linguistic groups can be seen in the eigenvector representation (Figure 19a) and the dendrogram (Figure 19b). It can also be seen that the Dani and Asmat are close to one another, while the Awyu are distinct from all of the other populations.

The regional homozygosity values for the combined Eastern and Western New Guinea populations (Table 29) all fall between the values for the two sets considered separately. ABO (.5054) gives the lowest value while the highest regional homozygosity is for the Tf system (.9066). The mean kinship values in this instance are very similar to those found in Eastern New Guinea and in Western New Guinea. For ABO, Phs, 6PGD and Hp the kinship values for the combined populations are higher than for either of the two sets of populations. The mean kinship is higher in Eastern New Guinea and lower in Western New Guinea than in the populations combined for MNS and PGM₂; the reverse is true for Tf. In the cases of the other two systems, Rh and PGM₁, the mean kinship values in both Eastern and Western New Guinea are higher than for the combined populations. That is, each set of populations considered separately shows more variation for these systems than does the combined set of populations. The lowest mean kinship is obtained for Tf (.0228) with the order of increase being Rh, PGM₂, Phs, ABO,

FIGURE 19a

Eigenvector Representation of Kinship Matrix for Eastern New Guinea and
Western New Guinea Populations

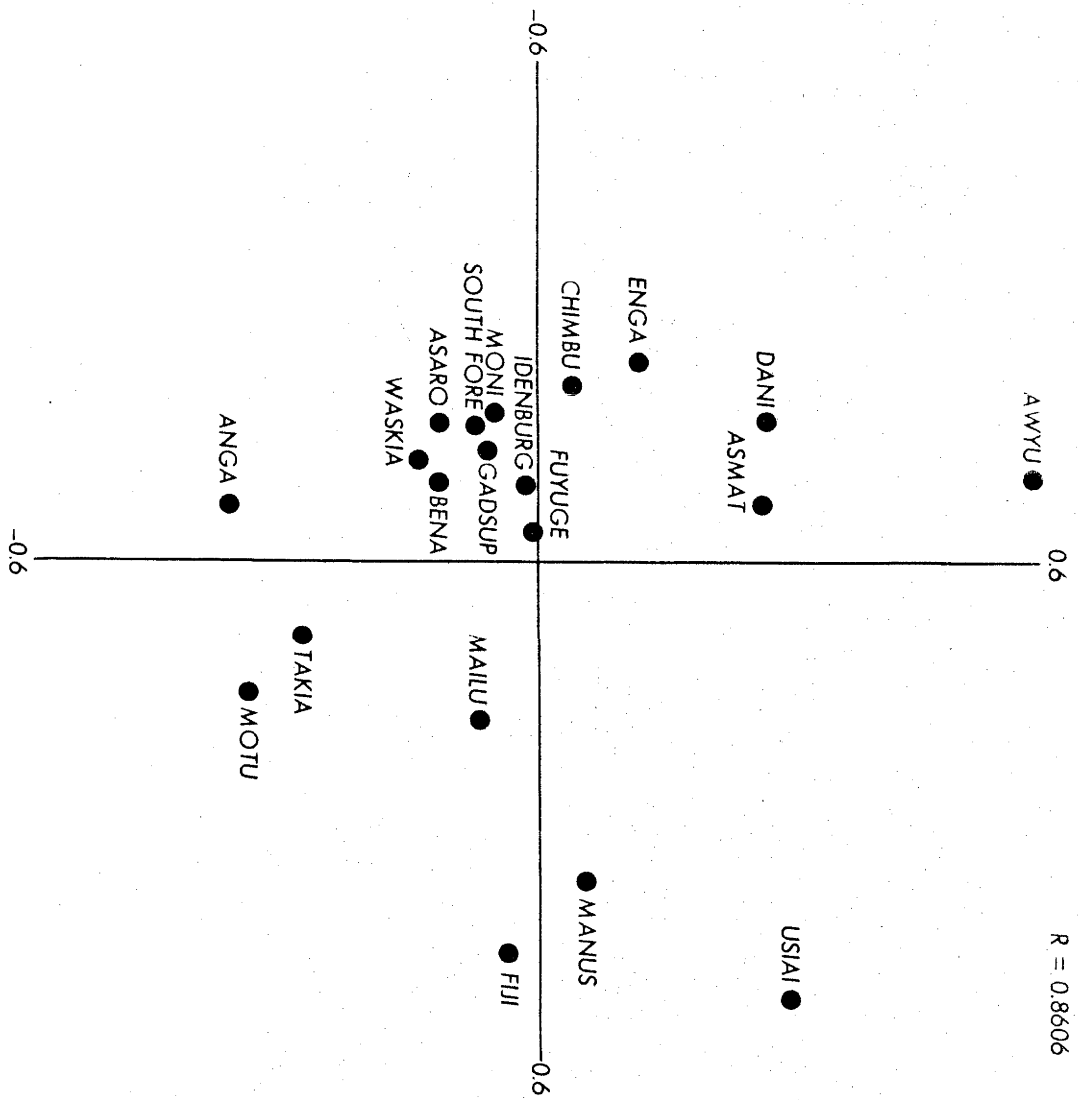


FIGURE 19b

Dendrogram from Kinship Matrix for Eastern New Guinea and
Western New Guinea Populations

$R = 0.8345$

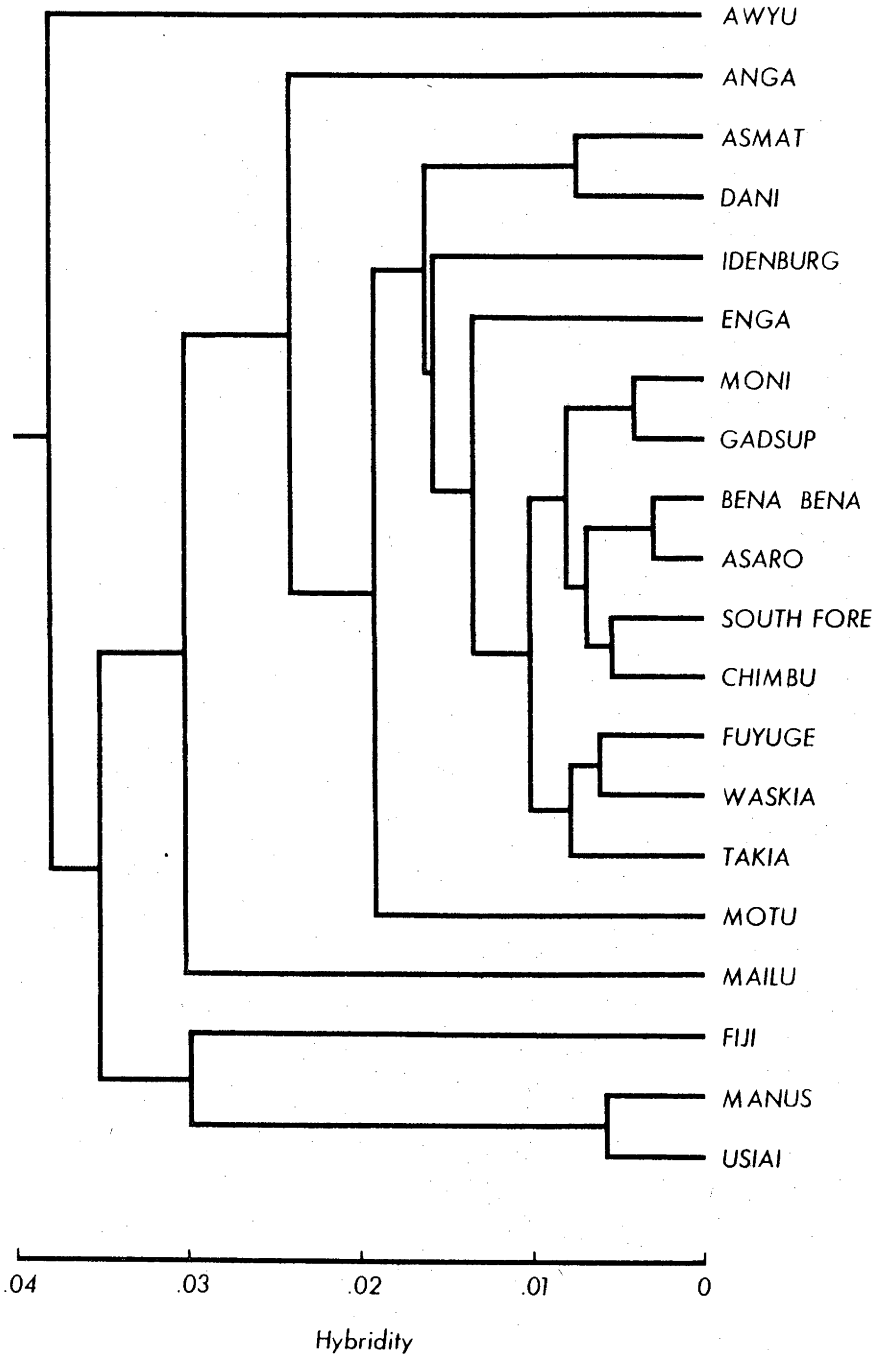


TABLE 30
 Kinship Between Australian Populations (with Eastern New Guinea and Western New Guinea included in the Regional Population)

	Doom.	M.I.	W.D.	Aranda	Walj.	Lurid.	Bid.	Malag	Nung.	Ranj.	Gun.	Tiwi
Doom.	.1427	.1557	.1373	.0966	.1649	.1393	.1962	.1213	.2046	.1090		
M.I.	.1233	.0572	.0924									
W.D.	.0673	.0770	.1194	.1039	.1395	.1418	.1322	.1234	.0884	.0985	.1109	
Aranda	.0795	.0851	.1282	.1066	.1429	.1055	.1244	.1032				
Walj.	.0747	.0712	.1040	.1200	.0949	.1393	.1213					
Lurid.	.0782	.0797	.0900	.1429	.1055	.1244	.1032					
Bid.	.0837	.0826	.0743	.0741	.0781	.0848	.0931	.1032	.0884	.0985	.1109	
Malag	.0813	.0777	.0750	.0752	.0840	.0821	.1057	.1068	.1156			
Nung.	.0673	.0960	.0459	.0405	.0495	.0431	.0623	.0642	.0630	.0708	.1369	
Ranj.	.0694											
Gun.	.0859											
Tiwi	.0906											

TABLE 31
Kinship between Eastern New Guinea Populations (with Australia and Western New Guinea
included in the Regional Population)

	Gadsup	Bena	Asaro	Sth. Fore	Chimbu	Enga	Anga	Fuyuge	Waskia	Mailu	Motu	Takia	Manus	Usiai	Fiji
Gadsup	.0251														
Bena	.0114	.0164													
Asaro	.0147	.0175	.0270												
Sth. Fore	.0142	.0101	.0109	.0209											
Chimbu	.0137	.0142	.0191	.0160	.0379										
Enga	.0252	.0204	.0185	.0160	.0337	.0671									
Anga	-.0052	-.0019	-.0087	.0068	-.0018	.0038	.0465								
Fuyuge	.0114	.0075	.0101	.0021	.0098	.0254	-.0019	.0224							
Waskia	.0108	.0079	.0098	.0076	.0223	.0322	.0048	.0138	.0290						
Mailu	.0006	.0088	-.0017	-.0069	.0093	.0200	.0022	-.0010	.0097	.0494					
Motu	-.0014	-.0055	-.0033	-.0128	-.0117	-.0102	-.0084	.0024	-.0001	-.0036	.0183				
Takia	.0059	.0067	.0014	-.0024	-.0005	.0116	.0092	.0105	.0069	.0109	.0060	.0184			
Manus	.0048	.0025	.0012	-.0155	-.0061	.0027	-.0145	.0116	.0039	.0138	.0134	.0117	.0809		
Usiai	.0055	.0005	-.0083	-.0159	-.0076	.0113	-.0167	.0121	.0013	.0273	.0084	.0154	.0814	.1135	
Fiji	-.0089	-.0041	-.0145	-.0074	-.0139	-.0115	-.0024	-.0058	-.0090	.0228	.0036	.0113	.0183	.0398	.0550

TABLE 32

Kinship between Western New Guinea Populations
(with Australia and Eastern New Guinea included
in the Regional Population)

	Asmat	Awyu	Moni	Idenburg	Dani
Asmat	.0337				
Awyu	.0475	.1302			
Moni	.0175	.0260	.0344		
Idenburg	.0188	.0228	.0115	.0567	
Dani	.0369	.0357	.0306	.0411	.0737

6PGD, PGM_1 , Hp to the highest value of .0698 for MNS. The populations in Eastern New Guinea show about the same amount of variation for each system as do those in Western New Guinea, and there are no large gene frequency differences between the two sets of populations.

Kinship Values Relative to the Total Region

When the regional population is taken as the three data sets combined (Australia, Eastern New Guinea and Western New Guinea), the kinship values between populations within countries would be expected to be greater than those obtained when only the country itself is considered. These values are shown in Table 30 for Australia, Table 31 for Eastern New Guinea and Table 32 for Western New Guinea. Comparing the results in Table 30 with those in Table 16 shows that for Australia the kinship is always higher when the New Guinea populations are included in the regional population. This indicates that the gene frequencies for all of the Australian populations are closer to the means for Australia than to the means for the

combined populations. For the Eastern New Guinea populations, although most of the kinship values are higher in Table 31 than in Table 18, there are a number of exceptions. The kinship within the Mailu, Motu, Usiai and Fiji decreases when the Australian and Western New Guinea populations are included in the regional population, and the kinship between pairs of these populations either decreases or remains about the same. This indicates that these Melanesian populations plus the Mailu are genetically more similar to a regional population comprising both New Guinea and Australia than to New Guinea alone. The results for the Anga are rather surprising. The kinship within the population and the kinship values between the Anga and other New Guinea groups are similar in both Tables 31 and 18. This indicates that the Anga show little relationship to either the New Guinea or the Australian populations. However, the Anga series was collected as part of a medical survey of the 'tropical splenomegaly syndrome' (Crane, 1972) and since it included a high proportion of patients it may not be representative of the Anga in general. On the other hand, linguistic studies (Wurm, 1975b) show that Anga is a Stock Family language with quite distinctive characteristics which make it likely that the people who speak Anga are themselves a genetically distinctive group. In the case of the Western New Guinea populations, the kinship values relative to the total region (Table 32) are all greater than those shown in Table 20 which presents results for the case when the regional population is just the Western New Guinea populations. As with Australia, the gene frequencies

of the Western New Guinea groups are all closer to the means for Western New Guinea than to the means for the total region.

Changes are also found in kinship values between populations in different countries when the total regional population is used. Most of the kinship values between populations in Australia and Eastern New Guinea in Table 33 (where Western New Guinea is included in the regional population) are about the same as those in Table 24. Exceptions are the Anga and the Melanesian populations paired with the Australian groups; these kinship values are greater in Table 33 than in Table 24. Therefore, when Non-Austronesian populations are added to the regional population, the relationships between the Melanesian and Australian populations become more pronounced. The Anga are again seen as an anomalous group.

The kinship between populations in Australia and Western New Guinea shows almost no change when Eastern New Guinea is included in the region (compare Table 34 with Table 26). Both sets of results suggest that there are no close genetic relationships between Australian and Western New Guinea populations.

The inclusion of Australia in the regional population leads to increases in the kinship values between Eastern New Guinea and Western New Guinea populations. This indicates that the gene frequencies for the New Guinea populations are closer to the mean gene frequencies for New Guinea than to the means for Australia and New Guinea combined. However, comparing Table 35 with Table 28 shows that there are some

TABLE 33

Kinship between Australian and Eastern New Guinea Populations
(with Western New Guinea included in the Regional Population)

	Doom.	M.I.	W.D.	Aranda	Walj.	Lurid.	Bid.	Malag	Nung.	Ranj.	Gun.	Tiwi
Gadsup	-.0378	-.0364	-.0401	-.0366	-.0431	-.0441	-.0511	-.0326	-.0317	-.0212	-.0287	-.0192
Bena	-.0290	-.0314	-.0199	-.0223	-.0280	-.0245	-.0284	-.0301	-.0278	-.0266	-.0313	-.0125
Asaro	-.0317	-.0337	-.0289	-.0286	-.0395	-.0319	-.0315	-.0300	-.0297	-.0223	-.0325	-.0109
S.Fore	-.0278	-.0420	-.0167	-.0245	-.0349	-.0199	-.0273	-.0216	-.0323	-.0164	-.0234	-.0227
Chimbu	-.0500	-.0590	-.0407	-.0430	-.0524	-.0434	-.0446	-.0492	-.0523	-.0456	-.0524	-.0463
Enga	-.0751	-.0652	-.0675	-.0660	-.0672	-.0715	-.0821	-.0720	-.0603	-.0555	-.0641	-.0515
Anga	-.0086	-.0087	.0067	.0035	.0032	.0066	.0001	-.0090	-.0085	-.0074	-.0106	-.0013
Fuyuge	-.0210	-.0177	-.0410	-.0255	-.0349	-.0382	-.0432	-.0292	-.0270	-.0225	-.0239	-.0112
Waskia	-.0333	-.0370	-.0413	-.0277	-.0402	-.0360	-.0381	-.0360	-.0415	-.0305	-.0354	-.0308
Mailu	-.0282	-.0202	-.0238	-.0151	-.0067	-.0153	-.0135	-.0338	-.0248	-.0225	-.0198	-.0275
Motu	.0184	.0283	-.0034	.0177	.0129	.0092	.0096	.0132	.0130	.0199	.0157	.0094
Takia	-.0054	.0058	-.0224	-.0056	-.0091	-.0169	-.0218	-.0216	-.0168	-.0166	-.0156	-.0005
Manus	.0058	.0115	-.0440	-.0144	-.0231	-.0312	-.0410	-.0270	-.0255	-.0152	-.0107	.0140
Usiai	.0029	.0130	-.0547	-.0270	-.0266	-.0441	-.0617	-.0449	-.0352	-.0302	-.0169	.0046
Fiji	.0313	.0467	-.0071	.0087	.0137	.0012	-.0060	-.0111	-.0071	-.0088	.0070	-.0012

TABLE 34

Kinship between Australian and Western New Guinea
Populations (with Eastern New Guinea included in
the Regional Population)

	Asmat	Awyu	Moni	Idenburg	Dani
Doom.	-.0433	-.0650	-.0462	-.0357	-.0534
M.I.	-.0538	-.0564	-.0369	-.0374	-.0621
W.D.	-.0529	-.0878	-.0407	-.0601	-.0679
Aranda	-.0464	-.0887	-.0440	-.0358	-.0611
Walj.	-.0532	-.0901	-.0445	-.0463	-.0671
Lurid.	-.0469	-.0986	-.0489	-.0479	-.0686
Bid.	-.0566	-.1017	-.0578	-.0528	-.0813
Malag	-.0476	-.0907	-.0415	-.0429	-.0598
Nung.	-.0494	-.0796	-.0327	-.0437	-.0591
Ranj.	-.0404	-.0888	-.0295	-.0298	-.0486
Gun.	-.0408	-.0773	-.0368	-.0346	-.0493
Tiwi	-.0326	-.0574	-.0110	-.0322	-.0428

TABLE 35

Kinship between Eastern New Guinea and Western
New Guinea Populations (with Australia included
in the Regional Population)

	Asmat	Awyu	Moni	Idenburg	Dani
Gadsup	.0141	.0140	.0223	.0230	.0312
Bena	.0104	.0186	.0151	.0094	.0098
Asaro	.0122	.0269	.0171	.0214	.0126
S.Fore	.0104	.0064	.0129	.0112	.0217
Chimbu	.0253	.0446	.0173	.0223	.0304
Enga	.0366	.0746	.0315	.0239	.0353
Anga	-.0037	-.0020	.0089	-.0148	-.0001
Fuyuge	.0134	.0258	.0127	.0127	.0157
Waskia	.0153	.0293	.0086	.0152	.0136
Mailu	.0135	.0217	.0120	-.0008	.0011
Motu	-.0097	-.0172	-.0064	.0051	-.0111
Takia	-.0008	.0003	.0094	.0032	.0008
Manus	.0137	.0117	.0041	.0107	.0035
Usiai	.0207	.0258	.0062	.0119	.0159
Fiji	-.0054	.0068	-.0112	-.0085	-.0076

TABLE 36

Regional Homozygosity and Mean Kinship
within Australian, Eastern New Guinea
and Western New Guinea Populations

System	Regional Homozygosity	Mean Kinship
ABO	.5265	.0531
MNS	.6418	.0831
Rh	.7162	.0745
Phs	.7311	.0858
6PGD	.8042	.0380
PGM ₁	.8275	.0456
PGM ₂	.8717	.0355
Hp	.5048	.2212
Tf	.8603	.0353

exceptions. The kinship values between the Motu and the Moni and Idenburg are lower in Table 35 than in Table 28, and, in general, the increase is not nearly as great for the Melanesian populations as for the Non-Austronesian groups. This again implies a genetic relationship between the Melanesian and Australian populations.

The regional homozygosity and mean kinship values for the total region are given in Table 36. It is clear from the results given in this table that the most variable system is haptoglobin which has both the lowest regional homozygosity and the highest mean kinship, while the least variable systems are transferrin and PGM₂.

The kinship matrix for all the populations in the region is summarized by the eigenvector representation shown in Figure

20a and the dendrogram in Figure 20b. These two diagrams show the three distinct groupings of Australian, Non-Austronesian and Melanesian populations, and, as well, the genetic relationship between the northern Australian populations and the Melanesian groups.

FIGURE 20a
Eigenvector Representation of Kinship Matrix for Australian, Eastern New
Guinea and Western New Guinea Populations

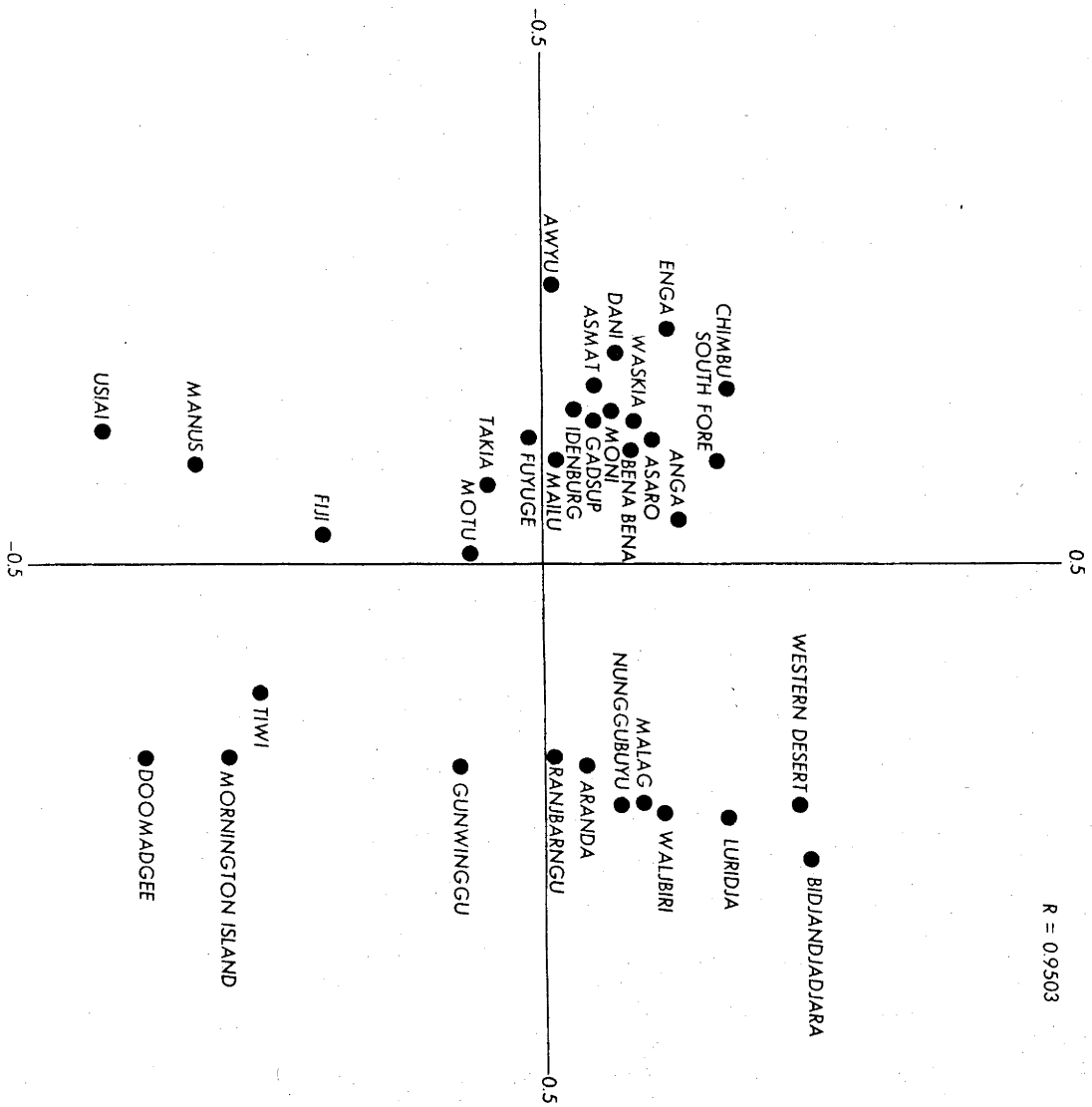
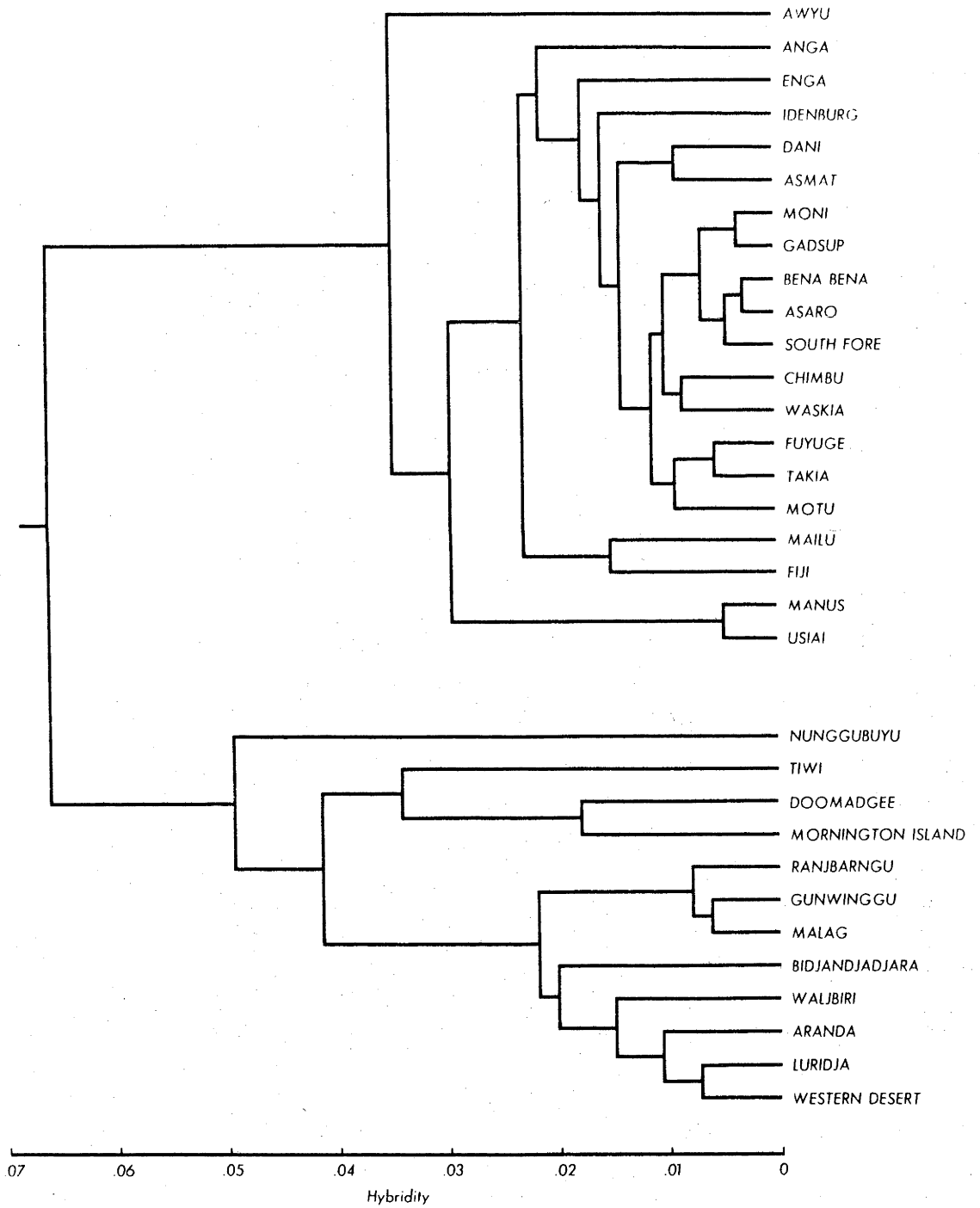


FIGURE 20b

Dendrogram from Kinship Matrix for Australian, Eastern
New Guinea and Western New Guinea Populations

R = 0.8323



Chapter 10

GENETIC DIFFERENTIATION: DISCUSSION

Interdisciplinary Evidence

The indigenous populations of Australia and New Guinea have features in common, however Howells' (1973) analysis of human skulls shows that, although they differ from other Pacific populations, they do not represent a single population. Linguistic and historical evidence (Wurm, 1975a) suggests that the Austronesian-speaking Melanesians, in contrast to the other established Papuan-speaking peoples, did not reach New Guinea until about 5,000 years ago. At this point of time Torres Strait had formed, so the genetic similarities of some Melanesian and northern Australian populations must be due to migration by sea.

The formation of Torres Strait marked the end of any major contact between the Australians and Non-Austronesians, and they may well have evolved separately for some time before that. The ancestors of the present day Australian Aborigines may have been in Australia for 50,000 years (Hope and Hope, 1976), whereas Wurm (1975a) claims that the original Papuan (Non-Austronesian) speakers began to spread throughout New Guinea from about 10,000 B.P. superimposing their language on ones already well established. The Non-Austronesian populations expanded through most of New Guinea and were probably not disturbed by outside influence until 5,000 years ago when the Melanesians arrived. According to Howells (1973) the Melanesians entered New Guinea from the west (perhaps from the Philippines or Indonesia) and moved along the north coast of New Guinea (where they probably came into close contact with Non-Austronesians) and then into Island

Melanesia. After moving into the Melanesian islands, they appear to have moved west again and reached areas around the mouth of the Markham River and localities on the south coast of New Guinea about 3,000 B.P.; during the last 2,000 years linguistic evidence suggests that Non-Austronesian languages and presumably genes have been carried into parts of Island Melanesia by Non-Austronesians who inter-married with Melanesians (Wurm, 1975a). Bellwood (1975), on the other hand, suggests that the Non-Austronesians may have reached the islands before the Melanesians arrived.

Justification of the Genetic Technique

The genetic distance technique used in this study is based on a small number of loci which are assumed to represent the whole genome. The blood samples tested from a population were usually not obtained using rigorous sampling techniques and therefore may not be a representative sample of the population; the error associated with the gene frequencies may be significant. However, the fact that the genetic and linguistic analyses are largely in agreement implies that the gene frequencies in populations today can be used to obtain answers to questions concerning relationships between populations in the past.

Justification of the technique is obtained from many of the results. For example, Wurm (1975a) showed that there is no linguistic similarity between the Australian and Non-Austronesian languages. The results of this genetic study show that there is no significant genetic relationship between peoples speaking these languages. Similarly, the intermixing of Non-Austronesians and Melanesians suggested by Wurm (1975a) on the basis of the presence of Austronesian loan words in Non-Austronesian languages is consistent with the genetic relationships of the

Mailu with the Melanesian groups. The Non-Austronesian highland group, Fuyuge, also shows genetic evidence of intermixing with the Melanesians.

Genetic and linguistic relationships between groups within linguistic types in the two countries are also consistent. For example, in Australia the Western Desert population clusters genetically with the Bidjandjadjara and the Luridja, and their languages belong to the same subgroup of the Pama-Nyungen family. Also the Malag, whose language belongs to the Pama-Nyungen family, are shown to be genetically related to the central populations although they are separated from them geographically. In New Guinea, the speakers of Bena Bena, Asaro and South Fore, which belong to the same family of the East New Guinea Highlands Stock, are closely related genetically, while the Anga group which is geographically close but linguistically different from the other eastern highland groups, is not closely related to them genetically. On the other hand, the Melanesian group from Fiji genetically clusters with the Melanesian populations from New Guinea even though they are separated by more than 3,000 kilometres. All of these Melanesian populations tend to cluster away from the Non-Austronesian speakers in the genetic analysis.

Effects of Geographic proximity on Genetic Differentiation

Geographic distances and ease of movement from one part of the country to another also affect genetic relationships between populations particularly in Australia. For example the Aranda group is geographically close to the Waljbiri and Luridja and it is also genetically related to these groups, although linguistically they belong to different groups of the Pama-Nyungen family. The Malag who are geographically close to the northern populations are related to them genetically, although

they are also genetically related to the central populations with whom they share a common language family. On the other hand, the island groups, Tiwi and Mornington Island, are much more difficult to reach than the mainland groups, and this isolation is seen in the genetic analysis. The ease of movement and the degree of contact between the Australian populations is shown by the fact that kinship decreases very slowly as distance increases. In New Guinea the kinship values fall off much more quickly as geographic distance increases, indicating that migration distances were much shorter than in Australia. For Eastern New Guinea the linguistic relationships are in much closer agreement than geographic proximity with the genetic differentiation between populations, and the decrease of kinship with geographic distance is not monotonic. Removing the Melanesian populations, which are separated by large distances geographically, does not change this result. In Western New Guinea the decrease of kinship is not as rapid as in Eastern New Guinea, but still much quicker than in Australia. For these populations, decrease in kinship corresponds in general to an increase in geographic distance. It therefore appears that movement in Western New Guinea was easier than in Eastern New Guinea, but more difficult than in Australia.

The Relationships between Melanesian and Australian Populations

Results from this genetic study also indicate that there has been migration between the Melanesians and the northern Australian Aboriginal populations. The direction of this movement is not clear, but the fact that the Melanesians are noted for their canoes and sea voyages (Bellwood, 1975) suggests that the Melanesian people crossed to Australia. These people may have been migrants from the Melanesian islands east of New

Guinea, some of whom landed on the south coast of New Guinea while others moved on to Australia, or they may have been people who had already lived on the New Guinea coast and later decided to explore and, in that way, reached Australia. Another possibility is that the relationship is due to the influence of the Macassans on both the Australian groups and the Melanesians. It is known that Macassan trepang fishermen made regular visits to the north coast of Australia (Macknight, 1972), while the Melanesians are thought to have entered New Guinea from around the area where the Macassans live, and traces of the Macassan language are found in the Melanesian languages (Wurm, 1975a). These migrations would explain the presence of the B gene of the ABO system, the red cell acid phosphatase Phs^a gene and some of the allogroups in the Gm system in northern Australia.

It is surprising that despite the genetic relationships between Melanesian and northern Australian populations, that there is no linguistic evidence of Melanesian influence on the Australian populations except for a negligible amount in south-east Arnhem Land (Wurm, 1975a). This suggests that the genetic analysis in this particular case is much more sensitive to contact between groups, and therefore, that the extent of contact between the Australians and the Melanesians was low. The Gm evidence, however, suggests a high rate of admixture (about 30%) (Steinberg and Kirk, 1970; Curtain *et al.*, 1976). This raises an interesting problem in the dynamics of cultural change. Aboriginal society has long been recognized as conservative, resisting the introduction of innovative techniques such as the planting and harvesting of seed. Possibly resistance to language change is another example of

this social conservatism among Aborigines. These results suggest that the combination of linguistic and genetic studies can be used to determine an important aspect of relationship, the degree of interaction between populations, in a finer-grained way than by using the results of either linguistic or genetic studies alone. This proposed technique may prove to be an important adjunct to the study of human population genetics.

Future Extensions of this Study

The results from this study of the extent of genetic differentiation among indigenous peoples of Australia and New Guinea suggest that the full advantage of genetic distance analysis is had when it is used in conjunction with independent information about relationships between the populations concerned. The decrease in genetic relationship with geographic distance, for example, should be looked at with regard to ease of movement through the region of study: What are the geographical barriers or political or social alignments that may hinder or foster movement of people? What is the ethnographic evidence for the existence of trade routes? Or what may have been the demographic factors which may have encouraged movement of people into or out of any particular area?

The combination of results from genetic and linguistic studies may be used to infer the extent of contact between populations. Blood genetic markers may indicate some contact in the past between populations which seem to be unrelated linguistically. Where oral or other historical records can be explored in detail, the presence of specific alleles may be traced to a single, or a limited number of introductions, as Morton and his colleagues have demonstrated for Micronesian atolls (Morton and Lalouel, 1973). A complete understanding

of the genetic relationships between populations in the present study area requires extension to neighbouring populations in Indonesia and other Western Pacific Islands.

Through the continued accumulation of data in related fields (archaeological to give estimates of time-depth, cultural and linguistic) and through combining information from blood genetic markers with that from other inherited traits, including anthropometric variables, it may be possible to add significantly to our understanding of the microevolutionary processes affecting the differentiation of human populations.

APPENDIX 1

Maningrida: Means, Standard Deviations and
Percentiles for Weight (kg)

Males:

Age	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
birth	100	2.878	.51	1.7	2.6	3.0	3.2	3.6
1 mth	89	3.888	.63	2.8	3.6	4.0	4.3	4.9
2 mth	97	4.867	.69	3.6	4.4	5.0	5.3	5.8
3 mth	101	5.667	.78	4.3	5.1	5.7	6.1	6.7
4 mth	102	6.312	.83	5.1	5.7	6.4	6.9	7.7
5 mth	102	6.845	.87	5.6	6.2	6.9	7.4	8.2
6 mth	101	7.274	.94	6.0	6.6	7.2	7.8	8.7
9 mth	100	8.019	.99	6.6	7.3	8.0	8.5	9.9
12 mth	97	8.504	.90	7.1	7.9	8.4	9.0	9.9
15 mth	91	8.979	.96	7.6	8.3	8.9	9.5	10.9
18 mth	86	9.526	1.00	8.1	8.7	9.5	10.1	11.3
21 mth	81	9.914	1.02	8.5	9.2	9.9	10.5	11.6
24 mth	73	10.548	.99	9.0	9.8	10.5	11.1	12.2
30 mth	64	11.444	.94	10.0	10.7	11.4	12.0	13.0
36 mth	50	12.112	1.20	10.2	11.1	12.0	12.9	14.1
42 mth	50	12.926	1.16	11.1	11.9	13.2	13.6	15.0
48 mth	50	13.696	1.28	11.8	12.7	13.7	14.7	15.6

Females:

birth	79	2.680	.39	2.0	2.5	2.7	3.0	3.3
1 mth	62	3.684	.49	2.8	3.4	3.7	4.1	4.3
2 mth	69	4.497	.56	3.3	4.2	4.6	4.8	5.3
3 mth	72	5.199	.66	3.9	4.8	5.3	5.6	6.2
4 mth	75	5.756	.75	4.2	5.3	5.9	6.2	6.9
5 mth	76	6.191	.81	4.9	5.7	6.3	6.8	7.5
6 mth	77	6.582	.79	5.2	6.1	6.7	7.1	7.8
9 mth	77	7.436	.83	6.0	6.9	7.4	7.9	8.7
12 mth	76	7.990	.81	6.8	7.5	8.0	8.4	9.3
15 mth	76	8.434	.80	7.0	7.8	8.4	8.9	10.0
18 mth	72	9.032	1.03	7.4	8.4	8.9	9.6	10.9
21 mth	72	9.500	.98	8.1	8.8	9.5	10.1	11.1
24 mth	72	10.035	1.05	8.2	9.2	10.0	10.7	12.0
30 mth	67	10.851	1.07	9.1	10.2	10.9	11.6	12.6
36 mth	61	11.775	1.24	9.9	11.0	11.8	12.5	13.6
42 mth	60	12.593	1.36	10.5	11.7	12.6	13.5	15.0
48 mth	57	13.335	1.29	11.0	12.6	13.2	14.2	15.3

APPENDIX 1 cont.

Bathurst Island: Means, Standard Deviations and
Percentiles for Weight (kg)Males:

Percentiles

Age	N	Mean	S.D.	5	25	50	75	95
birth	39	2.752	.36	2.3	2.5	2.6	3.0	3.5
1 mth	21	3.581	.45	2.9	3.2	3.6	3.8	4.2
2 mth	21	4.533	.53	3.8	4.1	4.5	5.0	5.3
3 mth	21	5.352	.59	4.5	5.0	5.3	5.7	6.2
4 mth	19	5.984	.71	4.5	5.6	5.9	6.6	7.1
5 mth	19	6.484	.73	5.2	5.9	6.5	7.0	7.9
6 mth	21	6.891	.96	5.7	6.1	6.9	7.4	8.1
9 mth	21	7.810	.90	6.7	7.3	7.8	8.4	9.2
12 mth	22	8.736	.71	7.7	8.2	8.7	9.2	9.8
15 mth	21	9.381	.62	8.5	8.9	9.3	9.7	10.2
18 mth	23	9.809	.74	8.7	9.3	9.7	10.4	10.7
21 mth	22	10.223	.71	9.3	9.7	10.3	10.7	11.6
24 mth	16	10.687	.66	9.7	10.0	10.8	11.0	12.1
30 mth	12	11.867	1.08	10.2	10.9	12.0	12.5	13.5
36 mth	12	12.600	.99	10.8	11.9	12.7	13.3	14.1
42 mth	10	13.470	1.06	12.2	12.5	13.8	13.9	15.3
48 mth	11	14.055	.90	13.1	13.2	14.3	14.6	15.9

Females:

birth	46	2.679	.54	1.8	2.3	2.6	3.1	3.6
1 mth	28	3.361	.68	2.1	2.8	3.5	3.8	4.3
2 mth	29	4.207	.79	2.8	3.9	4.3	4.9	5.3
3 mth	29	4.872	.88	3.2	4.4	5.0	5.6	6.0
4 mth	28	5.425	.96	3.6	4.8	5.5	6.2	6.6
5 mth	28	5.918	.94	4.4	5.2	6.0	6.7	7.2
6 mth	28	6.486	1.01	4.9	5.7	6.5	7.3	8.0
9 mth	25	7.088	.92	5.8	6.2	7.2	7.8	8.4
12 mth	19	7.984	.98	6.0	7.4	8.0	8.5	9.9
15 mth	18	8.733	.87	7.4	8.1	8.8	9.3	10.6
18 mth	19	9.421	.80	7.9	9.0	9.4	9.8	11.3
21 mth	19	9.953	.72	8.7	9.5	9.8	10.6	11.2
24 mth	15	10.307	1.00	8.7	9.4	10.5	11.1	11.7
30 mth	10	11.390	1.12	9.6	10.5	11.4	12.4	13.2
36 mth	10	12.510	1.34	10.4	12.0	12.4	13.1	15.2
42 mth	11	13.918	1.79	11.2	12.3	14.2	14.5	17.0
48 mth	13	13.915	1.43	11.8	13.0	13.7	14.6	16.9

APPENDIX 1 cont.

Milingimbi: Means, Standard Deviations and
Percentiles for Weight (kg)

Males:				Percentiles				
Age	N	Mean	S.D.	5	25	50	75	95
birth	19	3.069	.31	2.4	2.9	3.1	3.2	3.6
1 mth	10	3.850	.49	3.1	3.5	3.8	4.4	4.5
2 mth	10	4.710	.53	3.6	4.4	4.8	4.9	5.4
3 mth	10	5.640	.72	4.3	5.3	5.5	6.0	7.0
4 mth	10	6.150	.93	5.0	5.7	6.2	6.4	8.3
5 mth	10	6.410	.91	5.0	6.1	6.6	6.6	8.4
6 mth	10	6.770	.81	5.9	6.4	6.7	6.7	8.9
9 mth	10	7.510	.94	6.6	7.0	7.3	7.7	9.9
12 mth	13	8.208	.87	7.2	7.5	8.1	8.5	10.1
15 mth	11	8.691	1.02	7.4	7.7	9.0	9.7	10.3
18 mth	14	9.279	.93	8.1	8.5	9.4	9.9	11.3
21 mth	11	9.600	.75	8.8	8.9	9.3	10.5	10.8
24 mth	13	10.100	.79	9.0	9.5	9.8	10.9	11.3
30 mth	9	11.011	1.16	9.3	10.3	10.7	12.2	12.5
36 mth	9	11.933	1.29	10.2	11.0	11.8	12.7	14.0
42 mth	7	12.900	1.71	10.9	11.2	13.2	14.8	15.0
48 mth	3	13.467	1.46	12.3	12.3	13.0	15.1	15.1
Females:								
birth	20	2.693	.48	1.7	2.2	2.8	2.9	3.3
1 mth	14	3.543	.66	1.9	3.3	3.7	3.9	4.4
2 mth	14	4.564	.89	2.9	3.9	4.8	5.3	5.9
3 mth	14	5.236	.83	3.9	4.5	5.5	5.8	6.4
4 mth	14	5.757	.82	4.7	5.0	5.7	6.6	6.9
5 mth	14	6.150	.79	4.8	5.6	6.1	6.9	7.4
6 mth	15	6.673	.93	5.6	5.8	6.7	7.4	8.8
9 mth	13	7.246	.80	6.2	6.9	7.1	7.8	8.8
12 mth	12	7.592	.80	6.4	6.7	7.7	7.9	9.3
15 mth	12	8.325	.59	7.7	7.8	8.1	8.5	9.3
18 mth	13	8.700	.56	7.6	8.5	8.7	9.0	9.8
21 mth	11	9.164	.71	7.8	8.8	9.3	9.5	10.2
24 mth	9	9.467	.61	8.6	8.9	9.6	9.9	10.2
30 mth	6	10.117	.54	9.4	9.6	10.2	10.6	10.7
36 mth	6	11.183	.43	10.5	11.0	11.2	11.4	11.8
42 mth	5	11.880	.29	11.5	11.8	11.9	11.9	12.3
48 mth	4	13.275	.97	12.2	12.2	13.3	13.7	14.4

APPENDIX 1 cont.

Kowanyama full-bloods: Means, Standard Deviations and Percentiles for Weight (kg)

Males:

Percentiles

Age	N	Mean	S.D.	5	25	50	75	95
birth	35	3.017	.49	2.3	2.6	3.1	3.3	4.1
1 mth	32	4.300	.75	2.9	3.9	4.4	4.8	5.4
2 mth	32	5.259	.92	3.6	4.6	5.1	5.9	6.5
3 mth	33	6.036	1.10	3.9	5.5	5.7	6.8	7.5
4 mth	32	6.794	1.23	4.6	6.0	6.6	7.6	8.8
5 mth	33	7.315	1.33	5.0	6.5	7.0	8.2	9.6
6 mth	33	7.691	1.37	5.3	7.0	7.5	8.4	10.3
9 mth	30	8.643	1.10	7.2	7.8	8.7	9.0	10.8
12 mth	30	9.050	1.22	7.4	8.2	8.8	10.0	11.0
15 mth	30	9.513	1.28	7.8	8.5	9.2	10.5	11.4
18 mth	29	10.055	1.28	8.2	9.2	9.9	10.9	12.7
21 mth	28	10.536	1.36	8.7	9.3	10.4	11.5	12.9
24 mth	27	10.848	1.35	8.4	10.0	10.7	11.8	13.0
30 mth	26	11.977	1.28	9.8	11.3	11.8	13.0	14.0
36 mth	21	13.000	1.47	11.0	12.1	12.8	13.8	15.0
42 mth	15	14.033	2.14	10.9	13.0	13.9	15.9	19.1
48 mth	13	14.608	1.67	11.6	13.8	14.8	15.1	17.7

Females:

birth	30	2.874	.36	2.3	2.7	2.9	3.1	3.4
1 mth	26	4.089	.43	3.5	3.8	4.1	4.4	4.9
2 mth	27	4.830	.58	3.8	4.5	5.0	5.1	5.5
3 mth	29	5.548	.60	4.4	5.2	5.7	5.9	6.5
4 mth	27	6.233	.67	5.0	5.8	6.3	6.6	7.7
5 mth	27	6.707	.68	5.6	6.3	6.7	7.1	8.2
6 mth	28	6.971	.63	5.9	6.5	7.0	7.3	8.1
9 mth	28	7.804	.71	6.8	7.3	7.8	8.0	9.0
12 mth	27	8.407	.72	7.2	7.9	8.5	9.0	9.4
15 mth	27	8.937	.82	7.8	8.6	8.8	9.8	10.2
18 mth	25	9.356	.89	8.2	8.8	9.3	10.0	10.8
21 mth	24	9.900	.89	8.6	9.2	9.9	10.5	11.3
24 mth	23	10.304	.85	9.4	9.6	10.1	10.8	11.8
30 mth	19	11.453	1.02	9.2	10.6	11.6	12.1	13.5
36 mth	17	12.153	1.02	10.3	11.5	12.0	12.8	14.2
42 mth	13	13.054	1.01	11.3	12.5	12.9	13.7	15.1
48 mth	11	13.400	.94	11.6	12.8	13.5	13.9	15.3

APPENDIX 1 cont.

Kowanyama part-bloods: Means, Standard Deviations and Percentiles for Weight (kg)

Males:

Age	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
birth	23	3.022	.59	2.1	2.6	3.0	3.4	4.1
1 mth	19	4.295	.80	3.0	3.5	4.3	4.9	5.7
2 mth	20	5.205	1.09	3.0	4.2	5.3	6.2	6.5
3 mth	21	6.157	1.26	4.1	5.5	6.1	7.1	8.2
4 mth	21	6.852	1.41	4.6	6.3	6.7	7.9	9.3
5 mth	22	7.568	1.53	5.4	6.6	7.1	8.6	10.0
6 mth	22	8.032	1.51	6.2	6.7	7.8	9.2	10.5
9 mth	20	9.085	1.40	6.8	8.2	9.0	9.8	11.4
12 mth	17	9.694	1.66	6.8	8.6	9.6	10.8	13.0
15 mth	17	10.065	1.60	7.2	8.8	10.1	11.0	12.8
18 mth	16	10.687	1.58	7.9	9.6	10.6	11.6	13.2
21 mth	16	11.394	1.51	8.3	10.6	11.5	12.1	13.8
24 mth	16	12.019	1.75	9.0	10.9	12.2	13.3	14.9
30 mth	13	12.992	1.78	9.8	12.1	12.9	14.2	15.6
36 mth	10	14.110	1.72	11.3	12.7	14.1	14.9	17.3
42 mth	5	15.340	1.78	13.5	14.4	14.6	16.2	18.0
48 mth	5	16.480	2.28	14.1	15.3	15.9	17.0	20.1

Females:

birth	16	2.850	.49	1.9	2.4	2.9	3.2	3.6
1 mth	13	4.115	.70	3.0	3.8	4.2	4.3	5.5
2 mth	14	5.043	.92	3.5	4.6	5.0	5.7	6.9
3 mth	14	5.814	.96	4.3	5.4	5.7	6.5	8.1
4 mth	13	6.677	1.07	5.5	5.9	6.4	7.6	9.0
5 mth	13	7.208	1.13	5.6	6.4	6.7	8.4	9.4
6 mth	13	7.592	1.12	6.2	6.6	7.3	8.6	9.8
9 mth	13	8.162	1.19	6.8	7.1	7.6	9.3	9.9
12 mth	13	8.592	1.33	6.9	7.5	8.4	9.6	11.2
15 mth	11	9.036	1.39	6.9	8.3	8.7	10.2	11.8
18 mth	11	9.609	1.43	7.3	8.5	9.5	10.7	12.4
21 mth	10	9.880	1.40	6.9	9.0	10.0	11.1	11.6
24 mth	10	10.660	1.52	8.0	9.5	10.7	11.4	13.1
30 mth	9	11.278	1.47	8.9	10.3	11.4	12.4	13.6
36 mth	7	12.157	1.76	9.5	11.2	12.0	13.0	15.3
42 mth	6	13.000	2.03	10.4	11.8	12.8	13.8	16.4
48 mth	6	13.500	1.85	11.2	12.7	13.0	14.7	16.5

APPENDIX 2

Maningrida: Means, Standard Deviations and
Percentiles for Height (cm)

Males:

Percentiles

Age	N	Mean	S.D.	5	25	50	75	95
birth	52	48.4	3.2	43.0	46.5	48.5	50.0	54.0
3 mth	49	58.6	2.5	54.5	57.0	59.3	60.0	62.5
6 mth	49	64.7	2.4	61.0	63.0	65.0	66.0	69.0
9 mth	48	68.7	2.7	64.2	66.7	68.8	70.0	74.0
12 mth	47	72.5	2.4	68.5	71.0	72.5	74.6	76.0
15 mth	41	75.4	2.5	72.0	73.5	75.0	76.6	79.5
18 mth	38	77.9	2.7	73.0	76.0	77.8	80.0	82.2
21 mth	33	79.8	2.7	75.0	78.0	80.0	81.5	85.0
24 mth	34	81.8	2.9	77.0	80.0	81.8	83.5	87.0
30 mth	30	85.6	3.5	80.0	84.0	85.5	87.5	91.5
36 mth	23	88.7	2.6	85.0	87.0	88.5	91.0	92.5
42 mth	24	93.1	2.7	89.0	91.0	93.0	95.0	97.0
48 mth	24	96.6	2.7	92.0	95.0	96.8	98.5	101.0

Females:

birth	20	47.2	2.7	37.5	46.6	48.0	48.0	50.0
3 mth	19	57.7	1.8	54.5	57.0	58.0	59.5	60.2
6 mth	19	62.9	2.4	58.0	61.5	63.0	64.0	67.4
9 mth	18	67.2	2.1	63.2	66.0	67.0	69.0	70.4
12 mth	20	71.2	2.8	65.2	70.0	71.5	73.0	75.0
15 mth	20	74.6	2.4	70.0	72.7	74.5	76.5	78.0
18 mth	21	77.7	2.1	74.5	76.0	78.0	79.0	80.0
21 mth	20	79.9	1.6	77.5	78.5	79.8	80.6	82.5
24 mth	29	81.8	2.1	79.5	80.0	81.0	83.0	86.0
30 mth	30	85.6	2.3	82.5	84.0	86.0	87.0	89.0
36 mth	29	89.8	2.5	85.5	89.0	90.0	92.0	93.0
42 mth	31	93.7	2.9	88.0	92.0	94.0	96.0	98.0
48 mth	27	97.7	2.6	94.0	95.5	98.0	99.5	102.5

APPENDIX 2 cont.

Bathurst Island: Means, Standard Deviations and
Percentiles for Height (cm)

Males:				Percentiles				
Age	N	Mean	S.D.	5	25	50	75	95
birth	21	48.3	2.1	45.0	47.0	48.1	49.5	50.0
3 mth	21	58.5	1.7	56.3	57.0	58.3	59.5	61.0
6 mth	21	64.9	2.4	61.0	63.3	64.5	66.2	68.1
9 mth	21	68.7	2.1	65.5	67.7	68.8	69.7	71.8
12 mth	22	73.1	2.2	69.5	72.2	73.0	74.6	75.2
15 mth	21	75.9	2.0	73.5	75.0	76.0	77.3	78.2
18 mth	22	77.9	2.2	74.0	76.5	78.4	79.4	80.5
21 mth	21	80.2	2.2	77.0	79.0	80.6	81.6	82.7
24 mth	16	82.9	3.0	76.3	81.3	82.5	84.0	88.2
30 mth	12	87.0	2.5	83.3	85.0	86.0	89.0	90.7
36 mth	12	90.2	2.9	85.4	87.7	90.4	92.0	95.0
42 mth	10	94.3	3.4	89.8	91.5	94.1	98.0	98.4
48 mth	11	98.2	3.0	94.0	95.7	96.5	101.0	102.0
Females:								
birth	29	46.7	3.5	41.0	44.3	47.0	49.0	51.0
3 mth	28	56.1	2.9	51.3	54.0	56.2	57.5	61.2
6 mth	28	62.3	3.3	57.3	60.0	62.4	64.0	68.0
9 mth	25	66.8	3.1	61.7	64.5	66.4	69.5	71.4
12 mth	19	70.6	3.4	63.4	68.5	70.3	73.3	76.2
15 mth	18	73.4	3.3	68.0	71.2	73.3	75.7	79.0
18 mth	19	76.7	2.8	71.3	74.9	76.5	79.0	81.0
21 mth	19	78.7	3.1	72.7	77.3	78.2	81.0	84.8
24 mth	15	81.0	2.5	76.5	78.7	81.7	82.8	84.0
30 mth	10	85.3	3.5	79.0	85.0	86.0	88.0	89.0
36 mth	10	89.6	3.1	84.2	87.0	89.9	90.3	94.5
42 mth	11	94.7	4.2	86.0	92.2	94.4	97.8	100.5
48 mth	13	97.9	3.9	90.0	96.8	98.2	100.6	104.4

APPENDIX 2 cont.

Milingimbi: Means, Standard Deviations and
Percentiles for Height (cm)Males:

Age	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
birth	10	51.7	3.0	46.0	49.7	52.5	53.0	56.5
3 mth	10	60.2	1.8	56.5	59.2	60.5	61.5	62.0
6 mth	10	65.5	2.3	61.0	63.5	66.0	66.5	68.8
9 mth	10	68.4	2.2	66.2	67.0	67.3	69.5	72.3
12 mth	13	72.5	2.8	67.9	71.0	71.7	75.0	77.5
15 mth	11	75.1	2.0	72.5	73.6	75.0	76.0	79.0
18 mth	14	77.2	2.0	75.0	76.0	76.6	79.0	81.5
21 mth	11	79.2	2.1	77.0	77.5	78.8	80.0	84.0
24 mth	13	82.2	2.4	78.5	80.5	82.0	83.5	86.5
30 mth	9	85.7	3.9	80.5	83.0	86.0	87.5	91.2
36 mth	9	89.3	3.3	83.0	88.5	89.5	92.0	93.0
42 mth	7	93.1	3.9	85.5	91.5	93.6	96.0	97.0
48 mth	3	95.2	4.9	90.3	90.3	95.2	100.0	100.0

Females:

birth	14	49.0	3.2	42.0	47.0	49.8	50.5	54.0
3 mth	14	58.3	4.2	47.0	57.5	59.3	60.6	63.0
6 mth	15	64.3	1.6	61.2	63.0	64.2	65.0	67.0
9 mth	13	67.8	2.3	64.0	65.5	67.8	69.4	71.0
12 mth	12	71.7	2.5	67.0	69.5	72.0	72.5	75.1
15 mth	12	73.5	2.3	69.5	70.8	74.0	75.0	76.8
18 mth	13	76.3	3.1	71.2	74.2	76.5	78.0	82.7
21 mth	11	78.0	2.3	74.1	76.5	77.5	80.5	81.2
24 mth	9	80.2	1.7	77.5	79.0	80.5	81.1	83.0
30 mth	6	84.1	2.2	82.0	83.0	83.3	85.2	88.0
36 mth	6	88.3	1.8	85.7	87.5	88.0	89.5	91.0
42 mth	5	91.5	2.5	89.0	89.6	91.0	93.0	95.0
48 mth	4	97.6	2.4	94.5	94.5	98.0	99.0	100.0

APPENDIX 2 cont.

Kowanyama full-bloods: Means, Standard Deviations and
Percentiles for Height (cm)

Males:

Age	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
birth	22	49.4	3.4	45.5	45.5	49.5	51.0	54.5
3 mth	18	61.1	4.9	55.2	58.5	60.5	63.5	77.0
6 mth	23	67.1	5.3	61.0	64.5	66.0	69.0	79.5
9 mth	24	70.4	3.7	66.0	68.5	70.3	72.5	75.0
12 mth	24	73.9	3.2	70.5	71.5	73.8	75.0	77.5
15 mth	26	75.7	3.7	70.5	74.5	75.5	78.0	79.8
18 mth	28	77.9	3.3	73.5	75.2	78.0	79.5	82.0
21 mth	27	80.9	3.6	75.5	78.5	81.0	83.0	87.0
24 mth	26	83.3	3.9	76.5	80.2	83.3	86.0	90.0
30 mth	25	87.7	3.7	81.0	85.3	87.5	89.5	94.0
36 mth	22	91.9	3.7	86.5	90.0	91.0	94.5	98.0
42 mth	15	96.4	3.2	91.0	94.0	96.5	98.0	102.3
48 mth	13	99.4	3.7	93.0	98.0	99.8	100.5	106.0

Females:

birth	18	48.7	2.1	44.5	47.0	49.5	50.0	51.0
3 mth	14	58.6	2.1	54.0	57.5	58.5	60.0	62.0
6 mth	16	64.7	3.1	59.0	62.0	64.8	65.5	71.0
9 mth	18	68.8	3.2	64.5	65.5	68.8	70.5	74.0
12 mth	23	71.9	3.0	68.0	70.0	71.0	74.0	77.2
15 mth	23	75.3	2.5	72.5	73.0	75.0	76.5	79.3
18 mth	24	77.6	3.1	72.0	76.0	77.0	79.5	82.0
21 mth	23	79.8	3.3	76.0	78.0	79.0	81.5	86.0
24 mth	23	82.4	4.5	77.0	79.0	82.0	84.5	88.5
30 mth	19	85.8	2.6	82.0	84.0	86.1	87.5	92.5
36 mth	17	91.0	3.3	86.0	89.3	90.5	92.6	98.5
42 mth	13	94.7	3.1	89.0	92.9	94.5	97.5	98.5
48 mth	11	99.3	2.9	93.0	98.0	98.9	101.1	104.0

APPENDIX 2 cont.

Kowanyama part-bloods: Means, Standard Deviations and
Percentiles for Height (cm)

Males:

Age	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
birth	10	50.7	3.1	45.5	48.5	50.3	53.5	54.5
3 mth	12	60.2	4.6	53.5	55.5	61.5	62.0	68.0
6 mth	17	66.0	4.4	56.0	63.9	66.0	68.5	75.0
9 mth	17	70.7	3.0	65.0	69.0	71.0	72.0	77.0
12 mth	15	73.9	3.2	67.0	72.0	74.8	76.0	79.5
15 mth	15	76.2	3.4	68.5	74.5	77.0	78.5	81.5
18 mth	14	79.5	3.2	73.5	77.5	79.8	81.5	85.5
21 mth	15	82.5	3.7	75.0	81.0	83.0	84.5	89.8
24 mth	14	84.6	2.8	79.5	84.0	84.8	85.5	90.5
30 mth	12	89.9	3.5	84.0	86.0	90.0	91.0	96.5
36 mth	10	94.9	3.4	88.0	93.5	94.0	98.0	99.9
42 mth	5	98.1	3.1	95.0	96.0	96.5	100.9	102.0
48 mth	5	102.7	4.1	98.5	99.5	102.0	105.0	108.5

Females:

birth	5	48.0	3.0	43.0	48.5	48.5	49.0	51.0
3 mth	6	59.9	4.5	51.5	58.5	61.5	62.5	64.0
6 mth	7	65.3	3.5	62.0	62.0	64.5	69.0	71.0
9 mth	9	71.3	6.5	63.5	67.0	71.0	75.0	83.8
12 mth	9	72.3	5.3	65.0	69.0	72.5	76.5	81.0
15 mth	10	74.1	4.1	69.0	71.5	72.8	77.3	80.5
18 mth	9	76.3	3.9	72.0	74.0	74.5	80.0	83.0
21 mth	10	77.9	3.9	73.0	74.0	77.3	81.0	84.1
24 mth	10	81.1	3.8	76.0	79.0	80.8	82.0	88.5
30 mth	9	85.0	3.6	80.0	83.0	84.6	85.5	92.5
36 mth	7	89.1	2.8	84.0	87.5	89.0	91.0	92.5
42 mth	6	93.4	3.5	87.5	92.8	93.3	96.0	97.7
48 mth	6	97.9	3.7	92.5	96.3	97.3	102.0	102.0

APPENDIX 3

Maningrida: Means, Standard Deviations and
Percentiles for Head Circumference (cm)

<u>Males:</u>				Percentiles				
Age	N	Mean	S.D.	5	25	50	75	95
birth	52	33.4	1.4	31.0	32.4	33.5	34.5	35.0
3 mth	49	39.4	1.5	37.1	38.5	39.0	40.0	42.0
6 mth	49	42.1	1.2	40.0	41.5	42.0	42.5	44.0
9 mth	48	43.6	1.1	41.6	43.0	43.5	44.0	45.0
12 mth	47	44.8	1.0	43.6	44.0	44.5	45.5	47.0
15 mth	41	45.5	1.2	43.2	44.5	45.8	46.2	47.0
18 mth	38	46.3	1.1	44.5	45.5	46.5	47.0	48.2
21 mth	33	46.7	1.0	45.0	46.0	47.0	47.4	48.2
24 mth	33	47.1	1.1	45.5	46.5	47.4	48.0	49.0
30 mth	30	47.6	1.2	45.5	46.5	47.8	48.5	49.0
36 mth	23	48.0	1.3	46.0	47.2	48.0	49.0	50.0
42 mth	24	48.5	1.3	46.0	47.5	48.5	49.5	50.0
48 mth	24	48.9	1.2	47.0	48.5	49.0	49.5	50.8
<u>Females:</u>								
birth	20	33.1	1.5	29.0	32.0	33.0	33.5	35.0
3 mth	19	38.8	1.4	36.0	38.0	38.8	39.5	42.2
6 mth	19	40.8	1.4	38.3	39.5	41.0	42.0	43.0
9 mth	18	42.5	1.3	40.0	41.5	42.8	43.5	44.5
12 mth	20	43.8	1.2	41.2	43.0	43.8	44.5	45.5
15 mth	20	44.5	1.1	43.0	43.5	44.3	45.5	46.0
18 mth	21	45.1	1.0	43.5	44.5	45.0	45.5	46.5
21 mth	20	45.7	0.7	44.5	45.5	46.0	46.0	46.5
24 mth	29	45.9	0.8	44.5	45.5	46.0	46.5	47.0
30 mth	30	46.4	0.9	45.0	46.0	46.0	47.0	48.0
36 mth	29	47.0	1.0	45.5	46.2	47.0	48.0	48.0
42 mth	32	47.7	1.1	45.5	47.0	48.0	48.5	49.0
48 mth	27	48.2	1.1	46.0	47.5	48.2	49.0	49.5

APPENDIX 3 cont.

Bathurst Island: Means, Standard Deviations and
Percentiles for Head Circumference (cm)

<u>Males:</u>				Percentiles				
Age	N	Mean	S.D.	5	25	50	75	95
birth	21	33.6	0.9	32.0	33.0	33.8	34.4	34.9
3 mth	21	39.6	1.0	38.0	38.8	39.8	40.2	41.2
6 mth	21	42.3	1.3	40.8	41.2	42.4	42.7	44.8
9 mth	21	43.6	1.0	42.0	43.0	43.7	44.2	45.5
12 mth	22	45.2	0.8	44.2	44.8	45.1	45.6	46.8
15 mth	21	45.8	0.9	44.5	45.0	45.9	46.2	47.5
18 mth	22	46.2	1.0	44.8	45.6	46.1	46.8	48.0
21 mth	21	46.9	1.2	45.4	46.2	46.5	47.4	48.5
24 mth	16	47.3	1.1	45.2	46.3	47.4	48.0	49.5
30 mth	12	48.1	1.2	46.3	47.3	48.0	49.0	50.2
36 mth	12	48.9	1.8	46.3	47.7	48.4	50.0	52.8
42 mth	10	49.2	1.2	47.7	48.0	49.3	50.0	51.0
48 mth	11	49.0	1.2	47.0	48.3	48.8	50.0	51.0
<u>Females:</u>								
birth	28	32.9	1.8	30.5	31.0	32.9	34.0	35.8
3 mth	27	38.5	1.6	36.0	37.0	38.8	39.7	40.8
6 mth	28	41.2	1.7	38.5	39.8	41.3	42.5	43.4
9 mth	25	42.8	1.7	41.0	41.3	42.7	44.0	45.7
12 mth	19	43.8	1.3	41.3	43.0	43.9	44.7	46.7
15 mth	18	44.4	1.3	42.3	43.6	44.4	45.6	47.0
18 mth	19	45.3	1.2	43.0	44.5	45.5	46.0	48.5
21 mth	19	45.7	1.4	42.8	45.0	45.5	46.8	48.8
24 mth	15	46.1	1.6	43.0	45.4	45.9	47.0	49.6
30 mth	10	45.6	2.3	40.0	45.0	46.7	47.0	47.5
36 mth	10	46.8	1.3	44.0	46.3	47.0	47.5	49.0
42 mth	11	47.8	2.0	44.3	47.0	47.6	49.1	51.0
48 mth	13	47.3	1.4	45.0	46.5	47.0	48.0	50.2

APPENDIX 3 cont.

Milingimbi: Means, Standard Deviations and
Percentiles for Head Circumference (cm)

Males:				Percentiles				
Age	N	Mean	S.D.	5	25	50	75	95
birth	10	34.6	1.4	33.0	33.5	34.3	35.8	36.5
3 mth	10	40.3	1.3	38.0	40.0	40.0	40.5	43.0
6 mth	10	42.5	1.4	41.0	41.6	42.0	43.5	45.0
9 mth	10	44.1	1.6	42.0	43.4	43.8	44.5	47.3
12 mth	13	45.4	1.4	44.0	44.0	45.1	46.5	47.5
15 mth	11	46.3	1.3	44.9	45.0	45.8	47.5	48.5
18 mth	14	46.4	1.4	44.5	45.5	46.1	47.8	48.9
21 mth	11	46.4	0.9	45.5	45.5	46.3	46.5	48.2
24 mth	13	46.7	0.9	45.6	46.0	46.3	47.0	48.5
30 mth	9	46.9	1.2	45.8	46.0	46.5	47.0	49.0
36 mth	9	47.8	1.1	46.5	47.0	47.5	48.2	50.0
42 mth	7	48.0	1.0	47.0	47.0	48.0	48.4	50.0
48 mth	3	47.8	0.3	47.5	47.5	48.0	48.0	48.0
 Females:								
birth	14	33.5	1.7	30.0	32.5	34.2	34.7	35.5
3 mth	14	39.5	1.7	36.5	38.5	40.0	40.5	42.5
6 mth	15	42.1	1.3	40.5	41.0	42.0	42.9	45.5
9 mth	13	43.5	1.0	42.4	42.6	43.2	44.5	45.0
12 mth	12	44.2	0.7	42.8	43.8	44.1	44.5	45.5
15 mth	12	45.0	0.9	44.0	44.0	45.1	45.5	46.6
18 mth	13	45.5	0.9	44.1	45.0	45.6	46.0	47.7
21 mth	11	46.1	1.0	44.5	45.5	46.1	46.8	48.0
24 mth	9	46.2	0.9	44.8	45.8	46.1	46.5	48.0
30 mth	6	46.8	1.3	45.2	46.0	46.8	47.2	49.0
36 mth	6	47.3	1.1	46.0	46.5	47.0	48.0	49.2
42 mth	5	48.1	0.8	47.0	47.5	48.5	48.5	49.0
48 mth	4	48.0	1.2	46.8	46.8	48.1	49.0	49.0

APPENDIX 3 cont.

Kowanyama full-bloods: Means, Standard Deviations and
Percentiles for Head Circumference (cm)

<u>Males:</u>				Percentiles				
Age	N	Mean	S.D.	5	25	50	75	95
birth	4	36.5	1.0	35.0	35.0	37.0	37.0	37.0
3 mth	17	40.5	1.8	38.0	39.0	40.0	41.5	44.0
6 mth	23	43.0	1.5	40.7	42.0	43.0	44.0	45.0
9 mth	23	44.7	1.3	43.0	43.5	44.5	45.5	47.0
12 mth	24	45.7	1.6	44.0	45.0	45.7	46.5	47.5
15 mth	25	46.4	1.5	44.5	45.5	46.5	47.5	48.0
18 mth	27	47.1	1.4	45.0	46.0	47.5	48.0	49.5
21 mth	26	47.5	1.2	45.5	47.0	47.5	48.0	49.0
24 mth	25	47.9	1.3	46.5	47.0	47.5	48.5	50.0
30 mth	24	48.4	1.3	46.5	47.5	48.0	49.0	50.0
36 mth	22	49.1	1.5	46.8	48.5	49.0	50.0	51.0
42 mth	15	49.7	1.5	48.0	48.5	49.0	51.0	52.5
48 mth	13	49.4	1.6	47.0	48.0	49.0	51.0	52.0
<u>Females:</u>								
birth	6	35.5	2.5	34.0	34.5	34.5	35.0	40.5
3 mth	15	38.7	1.3	36.5	38.0	39.0	39.5	41.5
6 mth	17	41.8	0.9	40.0	41.0	42.0	42.5	43.5
9 mth	19	43.7	1.0	42.0	43.0	43.5	44.0	45.5
12 mth	23	44.6	1.0	43.0	44.0	44.5	45.5	46.5
15 mth	23	45.2	0.7	44.0	45.0	45.0	45.6	46.5
18 mth	24	45.5	0.8	44.0	45.0	45.5	46.0	46.5
21 mth	23	46.0	1.2	44.5	45.0	45.5	47.0	47.5
24 mth	23	46.4	1.2	45.0	45.5	46.0	47.5	48.0
30 mth	19	47.0	1.1	45.0	46.0	47.0	48.0	48.5
36 mth	17	47.4	1.4	45.1	46.5	47.5	48.0	50.5
42 mth	13	48.1	1.7	45.2	47.0	48.0	49.5	51.0
48 mth	11	47.7	1.3	45.6	47.0	47.5	48.5	50.0

APPENDIX 3 cont.

Kowanyama part-bloods: Means, Standard Deviations and
Percentiles for Head Circumference (cm)

Males:

Age	N	Mean	S.D.	Percentiles				
				5	25	50	75	95
birth	3	36.0	1.5	34.5	34.5	36.0	37.5	37.5
3 mth	12	40.6	2.5	35.0	39.0	41.3	42.0	44.0
6 mth	17	43.4	2.6	37.5	42.0	43.0	44.0	48.5
9 mth	17	44.9	2.4	39.0	44.0	45.0	46.5	49.0
12 mth	15	46.3	2.1	42.5	44.0	46.5	47.5	50.0
15 mth	15	47.3	2.0	44.0	46.0	47.5	48.5	51.0
18 mth	14	48.1	1.9	45.5	46.5	47.8	49.0	52.0
21 mth	15	48.4	1.9	46.0	47.0	48.0	48.5	52.5
24 mth	14	48.3	1.3	46.5	47.5	48.0	49.2	51.0
30 mth	12	48.8	1.6	47.0	48.0	48.5	48.6	52.0
36 mth	10	49.0	2.0	45.5	49.0	49.2	50.0	52.5
42 mth	5	51.0	1.5	49.5	50.0	51.0	51.0	53.5
48 mth	5	50.7	1.8	49.0	49.0	50.5	52.5	52.5

Females:

birth	4	33.9	2.2	32.0	32.0	33.3	33.5	37.0
3 mth	7	39.9	2.0	36.5	39.0	39.5	42.0	42.0
6 mth	7	42.7	1.5	40.5	42.0	42.5	43.4	45.5
9 mth	9	43.1	1.5	42.0	42.0	42.5	43.5	46.5
12 mth	9	44.2	1.6	42.5	43.0	44.0	44.5	47.5
15 mth	10	44.8	1.9	42.5	43.5	44.3	45.5	48.0
18 mth	9	45.1	1.3	44.0	44.5	44.5	45.5	48.0
21 mth	10	45.9	1.2	44.5	45.0	45.5	47.0	48.5
24 mth	10	46.5	1.1	45.5	45.5	46.0	47.5	48.5
30 mth	9	46.9	1.4	44.5	46.0	47.0	48.0	48.5
36 mth	7	47.6	1.1	46.0	46.5	47.5	48.5	49.0
42 mth	6	48.3	1.1	47.0	47.5	48.3	49.0	50.0
48 mth	6	48.3	2.4	45.5	47.5	47.5	49.0	52.5

APPENDIX 4

Statistical Techniques

In order to analyse the growth measurements of Australian Aboriginal children, several different statistical techniques were applied. Some of the computer programs used are packages available for use on the UNIVAC 1108 at the Australian National University, while others were written by the author. All of the data analysed are stored on magnetic tape at the Australian National University.

STATJOB

The STATJOB statistical analysis package was written at the Academic Computing Center, University of Wisconsin - Madison, and several of the computer programs included in this package have been used.

UNISTAT1 was used to test that data were normally distributed, and to calculate means, standard deviations and percentiles of data sets.

DSTAT2 was used to obtain correlations between variables.

ONEWAY1 was used to perform one-way analysis of variance.

Extensive documentation of these STATJOB analysis programs are available in the form of manuals which describe the input, output and the formulae used for the calculations performed by these programs.

BOX-JENKINS ANALYSIS PACKAGE

This package of computer programs has been developed at the University of Wisconsin and Ohio State University for the construction of univariate time series models using the methods described by Box and Jenkins (1970).

This analysis assumes that the observations, $z_t, t=1, 2, \dots, n$ of the time series are taken at equally spaced time intervals, and that they are correlated. A model is then determined from the autocorrelation and partial autocorrelation functions. The behaviour of these functions suggests whether the original series or one of its differences should be used, and it also provides clues about the type and order of the parameters, of which there are two types, autoregressive and moving average. An autoregressive process is one in which the current value of the process is expressed as a finite linear aggregate of previous values of the process and a shock a_t . For a moving average process, the current value is linearly dependent on a finite number of previous shocks.

The most general form of the model has an "autoregressive-integrated-moving average" (ARIMA) form,

$$(1 - \phi_1 B - \dots - \phi_p B^p)(1 - B)^d \dot{z}_t = (1 - \theta_1 B - \dots - \theta_q B^q) a_t$$

where B is an operator such that $Bz_t = z_{t-1}$; d is the number of differences and $\dot{z}_t = z_t$ if $d > 0$, $\dot{z}_t = z_t - \mu$ (series mean) if $d = 0$; $\phi_m, m=1, 2, \dots, p$ are the autoregressive parameters and $\theta_m, m=1, 2, \dots, q$ are the moving average parameters. This model is denoted as ARIMA(p, d, q).

The parameters are estimated by minimizing the sum of squares of the residuals or random shocks, and from these the fitted values of the series are determined, and future values are predicted.

Documentation is available describing the input, output and methods of the computer programs written for this time series analysis.

LEAST SQUARES FIT OF A POLYNOMIAL

The subroutine POLFIT described by Bevington (1969) was

used to fit the quadratic equation, $y = \alpha + \beta t + \gamma t^2$ to mean growth measurements. This subroutine uses the method of least squares to optimize the values of the coefficients α , β and γ . That is, the value of the weighted residual sum of squares (Q) is minimized by setting the derivatives of Q with respect to each of the coefficients equal to 0.

$$Q = \sum \left[\frac{1}{\sigma_i^2} (y_i - \alpha - \beta t_i - \gamma t_i^2)^2 \right] \sim \chi^2_{n-3}$$

where σ_i^2 is the variance of the i^{th} data point, and the number of degrees of freedom is $n-3$ where n is the number of data points.

In order to test whether the regression equations for two different sets of data are significantly different from one another, the regression equation for the two sets of data combined is calculated. In this case the residual sum of squares weighted by the variance has a chi-square distribution with $2n-3$ degrees of freedom. That is, let Q_1 be the sum of the weighted residual sums of squares for the two data sets considered separately, and Q_2 the weighted residual sum of squares for the two sets combined, then

$$Q_1 \sim \chi^2_{2n-6}, \quad Q_2 \sim \chi^2_{2n-3}$$

and $Q_3 \sim \chi^2_3$ where $Q_3 = Q_2 - Q_1$

The null hypothesis that the two regression equations are the same may then be tested by

$$\frac{Q_3/3}{Q_1/(2n-6)} \sim F_{3, 2n-6}$$

CONTOURING AND PLOTTING

The contouring subroutine used to provide a graphic representation of the correlation matrices was written by

Wolfe Data Processing of Madison, Wisconsin.

Plotting was done using the WPLOT computer program package from the University of Wisconsin.

STUDENT'S T-TEST

Suppose two samples of size N_1 and N_2 have means and standard deviations given by $\bar{X}_1$, $\bar{X}_2$ and s_1, s_2 respectively. The hypothesis that the population means are equal is tested by

$$t = \frac{\bar{X}_1 - \bar{X}_2}{\sigma \sqrt{1/N_1 + 1/N_2}} \quad \text{where} \quad \sigma = \frac{N_1 s_1^2 + N_2 s_2^2}{N_1 + N_2 - 2}$$

t has a Student's distribution with $N_1 + N_2 - 2$ degrees of freedom.

INTRACLASS CORRELATION COEFFICIENT

In some cases such as sibs and cousins there is no way of distinguishing between pairs. In order to calculate the correlation between such pairs, the intraclass correlation coefficient is used. It treats the pair of measurements symmetrically and is defined by

$$r = \frac{2 \sum_i (X_i - \bar{X})(X'_i - \bar{X})}{[\sum_i (X_i - \bar{X})^2 + \sum_i (X'_i - \bar{X})^2]}$$

where X_i and X'_i , $i = 1, 2, \dots, n$, are pairs of measurements and

$$\bar{X} = \frac{1}{2n} (\sum_i X_i + \sum_i X'_i)$$

APPENDIX 5

Genetic Distance Measures

Values of ϕ^* (Latter, 1973), θ (Morton *et al.*, 1971), f_α (Cavalli-Sforza, 1969), D (Nei, 1971, 1972), and d (Cavalli-Sforza and Edwards, 1967) for pairs of populations in Western New Guinea (Asmat, Awyu, Moni, Idenburg and Dani) using nine genetic systems (ABO, MNS, Rh, Phs, 6PGD, PGM₁, PGM₂, Hp, Tf)

	ϕ^*	θ	f_α	D	d
Asmat-Awyu	.0368	.0189	.0345	.0151	.3237
Asmat-Moni	.0197	.0100	.0345	.0066	.3238
Asmat-Idenburg	.0309	.0127	.0421	.0103	.3577
Asmat-Dani	.0138	.0061	.0220	.0048	.2588
Awyu-Moni	.0660	.0332	.1042	.0261	.5437
Awyu-Idenburg	.0854	.0391	.1120	.0343	.5638
Awyu-Dani	.0660	.0319	.0838	.0276	.4877
Moni-Idenburg	.0335	.0152	.0627	.0106	.4217
Moni-Dani	.0326	.0128	.0288	.0109	.2754
Idenburg-Dani	.0382	.0161	.0509	.0126	.3661

Standard errors were calculated for ϕ^* , f_α , and D . In all cases except one the standard error was less than half the distance value. The exception was for the value of D between Moni and Idenburg for which the standard error was .0061.

For each index the largest genetic distance is between Awyu and Idenburg and the smallest is between Asmat and Dani. The eigenvector representation and dendrogram obtained from each of the above genetic distance matrices were very similar to those shown in Chapter 8 for Western New Guinea.

APPENDIX 6

Sources of Published Gene Frequency Data

POPULATION	SYSTEM	REFERENCE
<u>Australia</u>		
Doomadgee	ABO, MNS, Rh	Simmons <i>et al.</i> (1964)
Mornington Island	Phs, 6PGD, PGM ₁ , PGM ₂ , Hp, Tf	Kirk <i>et al.</i> (1972a)
Western Desert	ABO, MNS, Rh PGM ₁ , PGM ₂	Kirk (1965b) Blake and Omoto (1975)
Aranda, Waljbiri, Luridja, Bidjandjadjara, Malag, Nungubuyu, Gunwingu, Ranjbarngu, Tiwi	ABO, MNS, Rh Phs, 6PGD, PGM ₁ , PGM ₂ , Hp, Tf	Simmons and Graydon (1971) Kirk <i>et al.</i> (1971)
<u>New Guinea</u>		
Gadsup	ABO, MNS, Rh	Simmons <i>et al.</i> (1972)
South Fore		
Chimbu	ABO, MNS, Rh PGM ₁ , PGM ₂	Simmons and Booth (1971) Blake and Omoto (1975)

APPENDIX 6 cont.

POPULATION	SYSTEM	REFERENCE
<u>New Guinea cont.</u>		
Enga	ABO, MNS, Rh, 6PGD, PGM ₁ , PGM ₂ , Hp, Tf	Sinnett <i>et al.</i> (1970)
Anga	ABO, MNS, Rh PGM ₁ , PGM ₂	Craggs <i>et al.</i> (1958) Blake and Omoto (1975)
Fuyuge	ABO, MNS, Rh, Phs, 6PGD, PGM ₁ , PGM ₂ , Hp, Tf	Woodfield <i>et al.</i> (1974)
Takia	ABO, MNS, Rh PGM ₁ , PGM ₂	Simmons and Booth (1971) Blake and Omoto (1975)
Manus Usiai	ABO, MNS, Rh, Phs, 6PGD, PGM ₁ , PGM ₂ , Hp, Tf	Malcolm <i>et al.</i> (1972)
Mailu, Waskia, Motu, Fiji	PGM ₁ , PGM ₂	Blake and Omoto (1975)
Dani	ABO, MNS, Rh Phs, 6PGD, PGM ₁ , PGM ₂ , Hp, Tf	Nijenhuis (1961) Kirk <i>et al.</i> (1973)

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Brief Communication:

GENETIC VARIATION AT THE THIRD LOCUS OF PHOSPHOGLUCOMUTASE IN PLACENTAS FROM AUSTRALIA AND PAPUA NEW GUINEA

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Summary. The frequencies of alleles at the third locus of phosphoglucomutase (PGM) have been determined by an electrophoretic examination of placental extracts for 205 white Australians, 101 Australian Aborigines and 191 Papua New Guineans. The PGM_3^2 gene was calculated to have a frequency of 0.22 in the white Australian sample, while for the Aborigines and Papua New Guineans the frequencies were 0.41 and 0.48 respectively. In order to obtain reproducible phenotypic patterns, it has been found necessary to preincubate the placental extracts with a solution of β -mercaptoethanol. Two of the Papua New Guinean samples had a new phenotype and this has been called PGM_3 3-1.

INTRODUCTION.

The enzyme PGM (E.C. 2.7.5.1.), which catalyzes the reversible transfer of phosphate from the first to the sixth position of glucose, is controlled by genes at three separate loci: only the products of genes at two of these loci can be detected in red cell lysates, but all three are found in extracts of various other human tissues, including leucocytes and placenta (Hopkinson and Harris, 1968; Lamm, 1969; Brinkman and Koops, 1971). Genetic variation at the two loci detectable in red cell lysates has been studied extensively, and all human populations are polymorphic at locus 1, but, with the exception of black African populations and the occurrence of rare variants elsewhere, are monomorphic at locus 2 (Hopkinson and Harris, 1966).

Since detection of PGM activity at the third locus requires the use of extracts from tissues other than red cells, relatively little information is available on the distribution of genetic variants at locus 3. So far 2 alleles, PGM_3^1 and PGM_3^2 , have been described in studies based on placental and leucocyte extracts. The PGM_3^2 frequency ranges from 23.6-26.6% in European populations (Hopkinson and Harris, 1968; Lamm, 1969; Monn and Gjonnaess, 1971; Herzog and Drdová, 1971), has a value of 66% for Nigerians (Hopkinson and Harris, 1968), but is only 19.1% in Japanese (Ishimoto, 1969).

The present report extends the study of genetic variation at the third locus of PGM to white and aboriginal populations in Australia and to an indigenous population in Papua New Guinea, and draws attention to some of the technical problems associated with accurate typing of PGM₃ phenotypes.

MATERIALS AND METHODS.

Pieces of placental tissue were obtained from white Australians after delivery at the Canberra Community Hospital. In the Northern Territory placental tissue was obtained at the time of delivery to full-blood Aborigines in Darwin Hospital and at the Government settlement at Maningrida, in Arnhem Land. Placental samples from Papua New Guineans were obtained from women delivering in the Port Moresby General Hospital. For both the Australian Aborigines and Papua New Guineans the series represented persons from a number of linguistic groups. The procedures for transport and preparation of placental extracts were those given by Blake, Kirk and Osathanondh (1968). Electrophoresis of placental extracts was carried out in 12% starch gels (Connaught Starch Hydrolysed) between metal cooling plates at approx. 10° and a voltage gradient of 4 v/cm for a period of 18 h. The buffer system used and the visualization of the PGM activity on the surface of the sliced gel followed the procedures of Spencer, Hopkinson and Harris (1964), modified to use an agar overlay. As indicated below, accurate typing of PGM₃ phenotypes was possible only after pre-incubation of placental extracts with β -mercaptoethanol.

RESULTS.

Under the conditions used normally for the study of electrophoretic variants of PGM, the PGM₃ activity is detected in the most anodal portion of the gel, and three phenotypes have been described in previous investigations. The PGM₃ 1-1 type possesses two bands, one on either side of the 'oxidase' zone: PGM₃ 2-1 has three bands, two corresponding to the 1-1 phenotype, the third being more cathodal. In the homozygote PGM₃ 2-2 this slower moving component is the most intense, the other two more anodal bands being either not detectable, or when faintly seen the centre band appears very slightly closer to the 'oxidase' zone than in the 2-1 phenotype.

When using simple placental extracts, either fresh or after storage at -20°, the clear-cut patterns described above were frequently not present, and difficulty was experienced in accurately typing the results. Experiments were carried out, therefore, to improve the resolution, and the following procedure has been found most satisfactory: to 0.1 ml of placental extract, 0.03 ml of 1:150 solution of β -mercaptoethanol in distilled water is added and the mixture allowed to stand at room temperature for a minimum of 60 min. This mixture is then applied to a double thickness of Whatman 3 mm filter paper (1.0 x 0.5 cm) and inserted into the gel in the normal manner.

Fig. 1 shows the three normal phenotypes for locus 3 in (a) untreated and (b) β -mercaptoethanol-treated placental extracts. It can be seen that the effect of β -mercaptoethanol is very striking on the 2-2 phenotype. The possible relationship between these changes and similar variation in band intensity at locus 2 in the same specimens has not been established so far.

Table 1 gives the distribution of phenotypes and the calculated gene frequencies for the three ethnic groups studied in the present investigation. All of these results were obtained from β -mercaptoethanol-treated extracts.

Based on 205 placental samples from white Australians and using a χ^2 test for the difference in gene frequencies, the PGM₃² frequency of 22.4% is not significantly different from the frequencies reported previously for northern and central Europe. The corresponding PGM₃² frequencies for 101 samples from Aborigines and 191 samples from Papua New

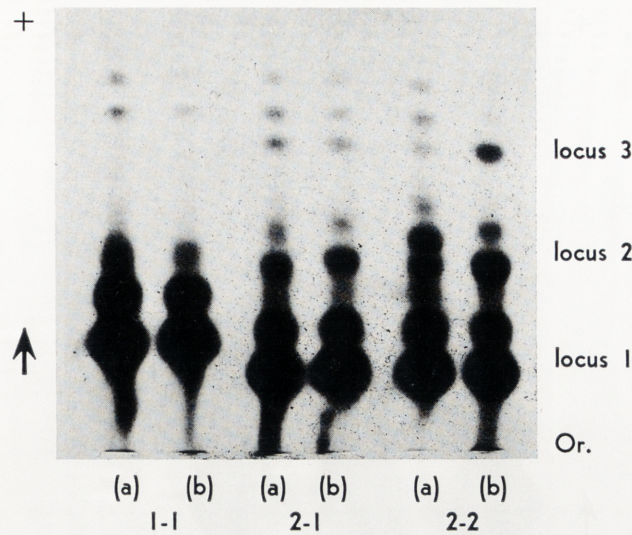


Fig. 1. Zymogram of PGM₃ activity showing the effect of β -mercaptoethanol on each of three phenotypes. The oxidase zone lies between the two bands of the 1-1 phenotype. In each case sample (a) is untreated while sample (b) is treated with β -mercaptoethanol.

Guineans are 41.1 and 48.4% respectively. Both these frequencies are significantly different from that for white Australians ($P < 0.001$), and Aborigines are also significantly different from Papua New Guineans ($P < 0.05$).

In addition to the three common phenotypes, two samples from Papua New Guinea gave an unusual pattern. As shown in Fig. 2, these two samples had a more anodal component additional to the two 1-1 components. The position and intensity of this faster moving component was not affected by treatment with β -mercaptoethanol, and we consider this pattern to represent a further variant at the PGM₃ locus, and it has been designated as PGM₃ 3-1.

TABLE 1.

	White Australians (Canberra)		Aborigines (Northern Territory)		Papua New Guineans (Port Moresby)	
	No.	%	No.	%	No.	%
<i>PGM₃</i>						
<i>Phenotypes</i>						
1-1	123	60.00	35	34.65	50	26.18
2-1	72	35.12	49	48.52	93	48.69
2-2	10	4.88	17	16.83	46	24.08
3-1	-	-	-	-	2	1.05
Total	205	100.00	101	100.00	191	100.00
<i>Gene frequencies</i>						
<i>PGM₃¹</i>	0.78		0.59		0.51	
<i>PGM₃²</i>	0.22		0.41		0.48	
<i>PGM₃³</i>	-		-		0.01	

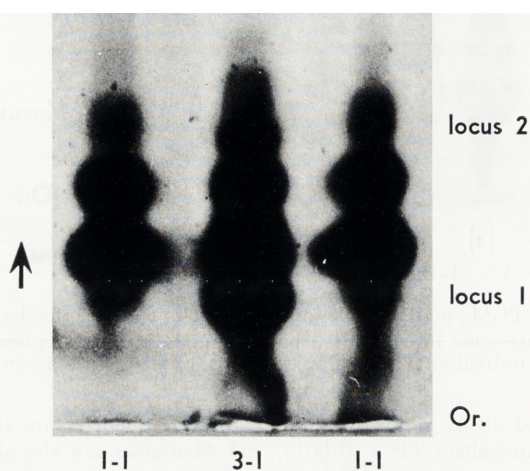


Fig. 2. Zymogram showing the variant PGM_3 3-1 phenotype compared with the PGM_3 1-1 phenotype. (All samples were treated with β -mercaptoethanol.)

DISCUSSION.

The work reported here indicates that simple extracts of placental tissue, after incubation with β -mercaptoethanol, can give reliable discrimination of genetic variation at the third locus of phosphoglucomutase, and has added further information on the gene frequencies of the common PGM_3 alleles in two additional ethnic groups. Further investigation of the PGM_3 polymorphism in other populations in South and South-East Asia and Oceania is in progress or is planned in the immediate future.

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Human microdifferentiation in the Western Pacific

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N.E. Morton and B. Keats

POPULATION STRUCTURE is a linear change in the frequency of heterozygotes from the value expected under panmixia. The definition traces to Wright (1921), who developed correlational and variance aspects, including multiple alleles and polysomy (Wright, 1938, 1951). 'This concept of Wright has enormously simplified population genetics, and its validity under a great variety of conditions is one of the great discoveries of mathematical biology' (Morton and Yasuda, 1963). It was left to Malécot (1948) to exploit the probabilistic interpretation in terms of kinship. Every year other measures of population structure are invented, which invariably reduce to some function of kinship. Any further analysis to describe isolation by distance, evolution of structure, or genetic topology is an operation on kinship, whether predicted from migration and genealogy or bioassayed from polymorphisms, metrics or isonymy.

Kinship

To approach microdifferentiation from the standpoint of kinship, let q_{ki} be the frequency of gene A^k in the i th population and $Q_k = \sum w_i q_{ki}$ be the regional frequency, where w_i is the contribution of population i to the region ($\sum w_i = 1$). For random pairs of gametes from populations i and j , the frequency of heterozygotes is $H_{ij} = 1 - \sum q_{ki} q_{kj}$. Under regional panmixia the frequency of heterozygotes is $H_0 = 1 - \sum Q_k^2$. By definition, kinship relative to the region is

$$(1) \quad \phi_{ij} \equiv (H_0 - H_{ij})/H_0 = (\sum q_{ki} q_{kj} - \sum Q_k^2)/(1 - \sum Q_k^2)$$

for $H_{ij} \neq H_0$ we may consider ϕ_{ij} the probability that a random gene in i be identical by descent with a random gene in j . More generally, within the region ϕ_{ij} is the correlation between the gene pools of i and j , and the expected covariance of the k th gene frequency in populations i and j is $Q_k(1 - Q_k) \phi_{ij}$. Thus identity by descent, correlation between gametes, and covariance of gene frequencies are intimately related.

Three properties of kinship are especially important in studying microdifferentiation. First, kinship ϕ_{ijR} within a region R is related to kinship ϕ_{ijT} within a larger collective T as

$$(2) \quad \phi_{ijR} = \frac{\phi_{ijT} - \phi_R}{1 - \phi_R},$$

where ϕ_R is the kinship of random gametes from the region relative to T . This is Wright's hierarchical description of population structure. Secondly, kinship declines approximately exponentially with distance d ,

$$(3) \quad \phi(d) \doteq (1 - L)ae^{-bd} + L$$

where a , b , L are the parameters of Malécot (1948).* In terms of the

* It is important to note that these parameters are characteristic of the local population: if demes are combined into tribes, prefectures, or other units larger than the breeding group, a and b will both be reduced.

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hierarchical model, $\varphi_R = -L/(1 - L)$. Thirdly, kinship increases in time according to

$$(4) \quad \varphi^{(t)} = \left[\frac{1}{4 N_e m_e + 1} \right] [1 - e^{-(2m_e + 1/2 N_e)t}]$$

where N_e is the evolutionary size of the population and m_e is the linearised systematic pressure (Morton *et al*, 1971a). This property is most useful when kinship is predicted from migration and genealogy, whereas the other properties can be studied either from predictions or by phenotype bioassay.

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Populations of the Western Pacific

Anthropologists on Pacific islands have collected data suitable for kinship analysis, but neither their work nor the large body of material from the western Carolines by Gajdusek and collaborators has yet been published in detail. An extensive study of Pingelap and Mokil atolls in the eastern Carolines was conducted by Morton and collaborators (reviewed in Morton, 1973a). A smaller study by Pollock *et al* (1972) on Namu atoll in the Marshalls and two surveys of Micronesia (Imaizumi and Morton, 1970; Morton and Lalouel, 1973) complete the kinship record for Oceanic populations (Table 1). The studies agree in showing kinship roughly equivalent to first cousins between random members of the same island (a) relative to all Micronesia. Decline of kinship (b) is slow, with no substantial decrease at distances of 100 km. Regular phenotypes (polymorphisms), metrics, and clan isonymy are in good agreement. The suggestion of Wright (1951), that human kinship is unlikely to exceed 0.02 even in isolates, is much too cautious.

N. Gajdusek

The evolutionary size of Oceanic populations is substantially smaller than their current census size (Table 2). This is because of population 'bottlenecks' during famines which followed typhoons and other disasters. Undoubtedly-restricted numbers of founders produced the same effect, with the consequence that archipelagoes populated from settlers on one atoll are expected to show as much drift as a small island. For example, phenotype bioassay gives a kinship of 0.0446 for random Marshallese, relative to all Micronesia. This is much greater than predicted from migration at the current population size, despite widespread voyaging which tended to fuse the scattered gene pool, as reflected both by anthropological accounts and the small value of b in Table 1 (Pollock *et al*, 1972; Morton and Lalouel, 1973). There seems little doubt that the Marshalls were populated from a small number of founders.

Natives of New Guinea show as much local kinship (a) as atoll dwellers, but the decline with distance (b) is much more precipitate, giving substantial decrease at 10 km and virtual abolition of measurable kinship at 100 km (Table 1). Clearly migrational distances are less in New Guinea than in Oceania, both because of geographic obstacles and hostility of neighbouring villages. Australian Aborigines have comparable values of local kinship (a) but much slower decline with distance (b), like Oceanic populations. Evidently geographic and social obstacles to long-distance migration were much less serious in Australia than in New Guinea, as the tradition of long treks and 'walk-about' suggests.

Table 1: Parameters of isolation by distance
 (after Morton, 1973a and ~~Kearse, 1974~~): $\phi(d) = (1 - L)ae^{-bd} + L$

Population	Source	L	a	b
<i>Oceanic</i>				
Micronesia	phenotypes	-.0081	.0463	.0023
	metrics	-.0133	.0569	.0016
	cognates	.1531	1	.0029
Pingelap/Mokil with others	phenotypes	-.0103	.0565	.0069
	metrics	-.0021	.0884	.0069
	cognates	.3440	1	.0045
	migration	0	.0606	.0120
	clans	-.0121	.0540	.0111
Marshall	migration	0	.0431	.0005
<i>New Guinea</i>				
Bougainville	phenotypes	?	.0765	.1050
	migration	0	.0588	.0954
New Guinea	phenotypes	-.0098	.0444	.0519
<i>Australian Aborigines</i>	phenotypes	-.0235	.0641	.0013

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Table 2: Parameters of kinship evolution (after Morton, 1973c)

Population	Source for m_e	Evolutionary size, N_e	Systematic pressure, m_e	Limiting kinship, Φ
<i>Oceanic</i>				
Pingelap	migration	87	.027	.0938
Mokil	migration	82	.076	.0341
Namu	genealogy	114	.045	.0468
<i>Other</i>				
Northeastern Brazil	genealogy	124	.308	.0065
Alpine isolates	migration	390	.092	.0060
Switzerland	migration	594	.160	.0021
Switzerland	genealogy	1499	.203	.0008

There are no estimates of evolutionary size and systematic pressure for New Guinea and Australia. However, the Malécot parameters suggest larger groups in New Guinea with less mobility than in Australia. This is of course only the genetic consequence of what anthropologists like Yengoyan (1968, 1970) have observed in Australia: small groups of 20 to 70 people, searching for food and water over an area of several hundred square miles with a kinship system that tends to provide access to resources by minimising hostility in group encounters. Among the swidden agriculturalists of New Guinea, inhabiting self-sufficient areas of higher density, peaceful relations with other groups are less advantageous and the social organisation fosters defense against encroachment.

Simulation of kinship

Two kinds of population structure have been predicted by a migration matrix. The simplest is a population subdivided by an exogamy rule into clans, moieties, and sections. Morton *et al* (1971b) considered a population of 160 adults of reproductive age with 5 per cent immigration from the outside world. The various marriage rules have almost no effect on random kinship in such a population, but inbreeding is increased by sections and circulating connubia relative to an undivided population, although not of course by comparison with group endogamy. If, as is likely, the society does not always follow an idealised system, the genetic effects must be even smaller than under this model. Therefore marriage rules appear to have a negligible effect on kinship, compared with population size and migration.

More complex structure has also been simulated, usually by estimating a migration matrix for actual populations. The number of tribes in the Western Pacific is too large for this method, but we may use a more abstract model. Suppose a region is composed of three populations, each of evolutionary size N_e and exchanging a proportion $k/2$ of its members with each of the other populations, called steppingstones. In addition, a proportion m is replaced each generation by immigrants from outside the region. Treating the local Australian population as a mob of several bands, we took $N_e = 98$ from Table 2 and $m = 0.02$ from the suggestion of Tindale (1953) that 7.5 per cent of marriages contracted among Australian Aborigines prior to appreciable White influence were intertribal. A similar value is indicated for New Guinea (Friedlaender, 1971) and Oceania (Table 2).

Malécot (1948) deduced that systematic pressure is

$$(5) \quad m_e \doteq \sqrt{m(m + 2k)}$$

Equation 4 gives for local kinship

$$a \doteq \frac{1}{4N_e m_e + 1}$$

These relations allow us to estimate

$$(6) \quad \begin{aligned} m_e &\doteq (1 - a)/4a N_e \\ k &\doteq (m_e^2 - m^2)/2m \end{aligned}$$

Only the effective size N of the population is undetermined. However, Morton *et al* (1971a) found that the ratio $C = N_e/N$ is insensitive to changes in N . Therefore by simulating structure with a migration matrix at a trial value N_0 , with corresponding local kinship a_0 , we can determine $N = a_0(1 - a) N_0/a(1 - a_0)$ and verify other parameters under the model.

Table 3 gives these results. The systematic pressure due to migration is many orders of magnitude greater than mutation and selection rates determined from amino-acid substitution. The possibility of inferring selection pressure from geographical distribution of gene frequencies is remote, unless the agent of selection (malaria, etc.) can be determined on other evidence. The chance of making a critical test of neutral mutation is negligible.

The inbreeding coefficient is close to local kinship on the assumption that mating between a given pair of populations is random. Under the population structure of the Western Pacific elimination of deleterious 'recessive' genes must have been largely through inbreeding, not heterozygote disadvantage as has been suggested for farming and industrial populations (Morton, Crow and Muller, 1956). The effective size is less than the evolutionary size. Oceania, New Guinea, and Australia do not differ much in local kinship, evolutionary size, or systematic pressure. However, stepping-stone distance ~~4-4~~ hundreds of kilometres in Oceania and Australia but only a few kilometres in New Guinea. The genetic structure reflects the main features of ecology and social organisation.

Other indices of structure

If x_i is the vectorial deviation of population i from the regional mean, then $x_i x_i'$ is a measure of *affinity* (similarity) and $(x_i - x_j)(x_i - x_j)'$ is a measure of *divergence* (dissimilarity). Kinship, correlation, and Wright's F statistics are examples of affinity, while genetic distance typifies divergence. Affinity decreases with geographic distance, and divergence increases. Affinity between a population and its founders (or between two populations with a common origin) decreases with time, whereas divergence increases. Of course, affinity within a contemporary population or between two independent populations under migration increases with time, just as divergence does, a circumstance that has led to confusion between kinship and distance (Cavalli-Sforza, 1973). The two concepts have a simple relation, since

$$(x_i - x_j)(x_i - x_j)' = x_i x_i' + x_j x_j' - 2 x_i x_j'$$

In words, the divergence between two populations is the sum of their internal affinities, minus twice their cross affinity. In the case of kinship,

$$(7) \quad D_{ij} = \varphi_{ii} + \varphi_{jj} - 2 \varphi_{ij}$$

where D_{ij} is the genetic distance. It is easy to show that Mahalanobis' distance equals D_{ij} except for a proportionality constant which is a function of genetic covariances (Morton, 1973a). Kullback (1968) derived Mahalanobis' distance from information theory, and so genetic distance has a strong theoretical foundation.

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Table 3: Simulation of kinship

Parameter	Oceania	New Guinea	Australian Aboriginals	Northeastern Brazil	Switzerland	Alpine isolates
Assumed:						
long-range migration, m	.04	.02	.02	.20	.10	.05
local kinship, a	.0580	.0600	.0641	.0050	.0025	.0069
Malécot exponent, b	.0054	.0841	.0013	.0021	.0185	.0643
stepping-stone migration, k	.0123	.0500	.0420	.3024	.0881	.0560
effective size, N _e	75	87	85	75	491	372
Predicted at t = 1:						
kinship with stepping-stone, ϕ_m	.0080	.0354	.0346	.0034	.0009	.0027
inbreeding coefficient, α	.0568	.0580	.0620	.0040	.0022	.0064
stepping-stone distance, $D = \ln(a/\phi_m)/b$	364	6	475	180	54	14
Verified by equation 4:						
evolutionary size, N _e	80	108	98	178	649	447
systematic pressure, m _e	.0509	.0362	.0371	.2825	.1649	.0806

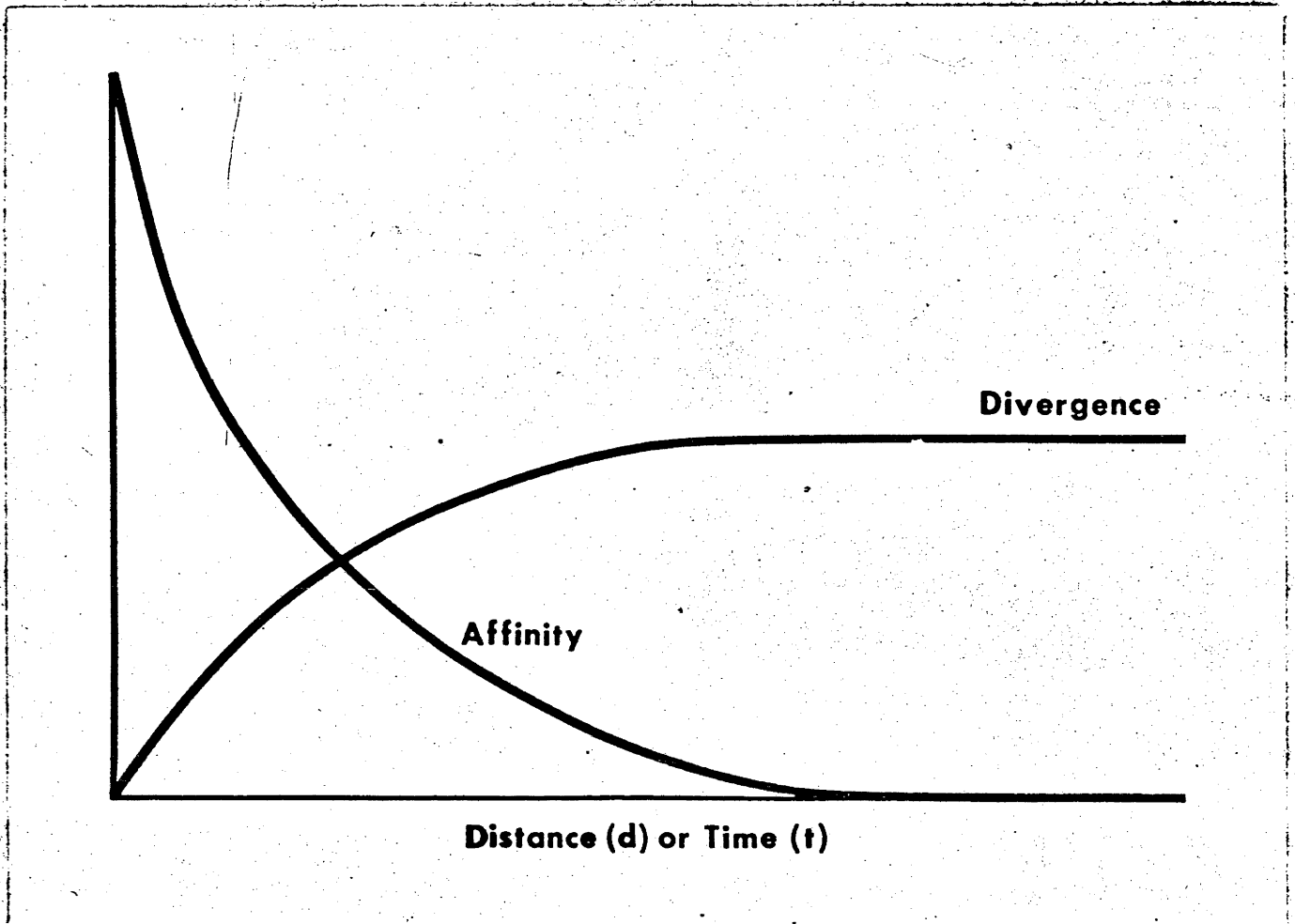


Fig. 1. Affinity and divergence

There is, however, a slight disadvantage to D_{ij} . Applying equation 3, we see that

$$(8) \quad D_{ij} \doteq 2a(1 - e^{-bd})(1 - L)$$

The scalar L is no obstacle to microtaxonomy, but for comparison of different structures, it is better to use the hybridity,

$$(9) \quad \theta_{ij} = \frac{\varphi_{ii} + \varphi_{jj} - 2\varphi_{ij}}{4 - \varphi_{ii} - \varphi_{jj} - 2\varphi_{ij}}$$

which has expectation

$$E(\theta_{ij}) = \frac{a(1 - e^{-bd})}{2 - a(1 + e^{-bd})}$$

and therefore is invariant with respect to L . Hybridity has a simple genetic meaning. If H_2 is the heterozygosity in the F_2 between two populations, then the F_1 heterozygosity is

$$(10) \quad H_1 = (1 + \theta_{ij}) H_2$$

and the heterozygosity in the two parental populations is

$$H_0 = (1 - \theta_{ij}) H_2$$

This property is appealing, but since $1 - L$ within a region is not much different from unity, in theory and practice there is little to choose between θ_{ij} and $D_{ij}/4$.

Nei (1973) has devised a set of statistics based on local homozygosity, $\sum q_{ki} q_{kj}$. He calls $H_T = 1 - \sum Q_k^2$ the gene diversity of the total population, and $D_{ST} = \sum w_i w_j q_{ki} q_{kj}$ the gene diversity between populations. Then $G_{ST} = D_{ST}/H_T$ is the relative measure of gene differentiation. It is easy to show that

$$G_{ST} = \frac{\varphi_0 - \varphi_R}{1 - \varphi_R}$$

where

$$\varphi_0 = \sum_{i,k} w_i q_{ki}^2$$

and

$$\varphi_R = \sum_k Q_k^2$$

Thus G_{ST} is the mean kinship within populations, relative to the region, which is identical to the F_{ST} of Wright (1921), the φ of Morton *et al* (1971c), and the R_{ST} of Workman *et al* (1973). In terms of Malécot parameters, equation 3 gives $G_{ST} = (1 - L)a + L$ (Morton, Miki and Yee, 1968). As the mean of the diagonal of a kinship matrix, G_{ST} summarises a symmetrical matrix of rank n by a scalar, and therefore less completely than the Malécot parameters, which give not only G_{ST} but also the decline of the off-diagonal entries with distance.

Latter (1972) proposed the statistic

$$\begin{aligned} \varphi^* &= \frac{2\theta}{1 + \theta} \\ &= \frac{\varphi_{ii} + \varphi_{jj} - 2\varphi_{ij}}{2(1 - \varphi_{ij})} = \frac{a(1 - e^{-bd})}{1 - ae^{-bd}} \end{aligned}$$

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$1 - \sum w_i q_{ki}^2 - \sum Q_k^2$

delete

In the absence of systematic pressure $a = 1$, and then $\varphi^* = a$. However, systematic pressure from migration, mutation, and perhaps selection is ubiquitous, and so φ^* seems poorly motivated. He also suggested an 'index of mutational divergence'

$$\gamma_{ij} = 1 - \frac{2\varphi_{ij}}{\varphi_{ii} + \varphi_{jj}} \\ \doteq 1 - e^{-2\mu t} \doteq 2\mu t$$

for $\varphi_{ij} = \sum q_{ki} q_{kj}$, where μ is the mutation rate per generation since the population separated t generations (or years) ago. This would be appropriate for populations of uniform size if migration and selection pressure were negligible relative to mutation. As Table 2 shows, the condition does not hold within our species, and probably within any species, although it may apply to higher taxa over phylogenetic sequences short enough so that $1 - e^{-2\mu t} \doteq 2\mu t$.

Clearly all these indices of population structure are simple functions of the kinship matrix.

Genetic topology

Studies of population structure have two objectives: (1) to compare different structures, for example with respect to Malécot parameters, and (2) to describe kinship among populations within a region. The latter is called *genetic topology*. It commonly takes the form of a two-dimensional graph, which gives more detail than summary indices like Malécot parameters or F statistics, but sacrifices some of the information in the kinship matrix (φ_{ij}) in order to demonstrate its main features. In one type of graph each population is represented by a point, with similar populations tending to cluster. Diversity among populations is maximised by taking the axes as the principal components of the centroid-adjusted kinship matrix (Lalouel, 1973). The other type of graph is a bifurcating tree in which more similar populations are separated by shorter paths. The logical structure is not altered by rotating any branch 180°, so that $A(BC) = A(CB) = (BC)A$. A tree constructed on affinity or divergence, without phylogenetic assumptions, is called a *dendrogram*. A tree constructed on the assumption of evolution with binary fission but no migration is called a *cladogram*. The main axis of a dendrogram is distance or hybridity, which in a cladogram may be converted to time since divergence began on the assumption of uniform drift. There are many competing algorithms for constructing a tree, which can be objectively compared in terms of the cophenetic correlation between observed and expected distance or hybridity. Numerical taxonomy (Sokal and Sneath, 1963) and recent genetic experience (e.g. Martin, 1973) have urged caution in interpreting a dendrogram as a cladogram, especially at the subspecific level (Morton and Lalouel, 1973).

Imaizumi *et al* (1973) studied the genetic topology of 25 polymorphisms in 25 populations with the results shown in Figure 2. The Western Pacific is a distinct cluster of populations, with greatest affinity to the Mongoloids of South East Asia.

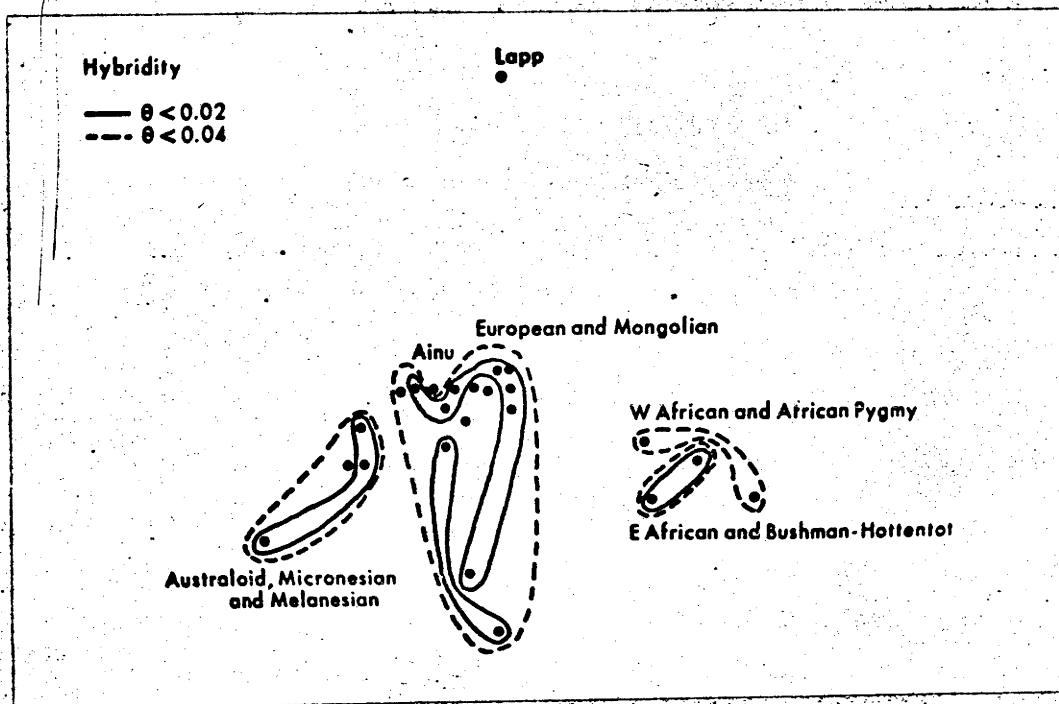


Fig. 2. Principal components of hybridity in 25 races
(after Imaizumi et al. 1973)

To examine the topology of this region more closely we chose 13 polymorphisms in 17 populations, mostly from the Western Pacific (Figure 3). The gene frequencies are set out in Table 4. Because of a question raised by Latter (1973), kinship was calculated from gene frequencies by two methods. In the first, each system was treated separately and the kinship estimates pooled, with equal weights (Table 5). In the second, the quantities $\sum_k Q_k^2$ and $\sum_k q_{ki} q_{kj}$ were averaged over systems and kinship was computed from these means. These estimates will be called within and among systems, respectively.

The principal components analysis is almost indistinguishable for the two methods, with a correlation of 0.935 within systems and 0.926 among systems. The Ainu cluster with the Mongoloid populations, and there is no similarity between Melanesians and Negroids (Figure 4).

A tree representation conserves these features, but the cophenetic correlation is reduced to 0.783 within systems and 0.808 among systems. Figure 5 gives the former tree as a cladogram, assuming exponentially linear differentiation from the first split 100,000 years ago. Comparison with the principal components plot, which conserves more of the information in the kinship matrix, makes one properly cautious about a phylogenetic interpretation. The most striking feature of these analyses is the diversity among Australoids, Micronesians, Melanesians, and Polynesians, which may indicate a small founder population, a long time span, or both.

Significance of polymorphism

Inspection of Table 6 shows that mean kinship within populations is about 0.05 for systems like Gc, PGM, ABO, Tf, and Inv, but reaches much higher values for Gm, Fy, and Rh. Imaizumi *et al* (1973) reported similar values for world populations. This variation may be due to differences among loci in rates of mutation, selection pressure, time since last fixation, stochastic departure from equilibrium, or power to detect genetic differences by electrophoretic or antigenic methods. The alternatives to a null hypothesis of uniformity are so numerous that the fact of variability gives no information about the relative importance of selection and neutral mutation.

The mean kinship for these systems is about 0.15, with a variance that is minimal for the estimator ϕ_A given by equation 1. The estimator

$$\phi_{ij} = \left\{ \sum_{k=1}^A q_{ki} q_{kj} / Q_k - 1 \right\} / (A - 1)$$

and the Malécot estimator $(1 - L) a + L$ give similar means with slightly larger variances. The largest error is associated with regional homozygosity.

Kinship among systems is

$$\phi = \frac{.7024 - .6366}{1 - .6366} = .1811$$

which is greater than any of the estimates based on system means.

If we allow for monomorphisms at 72 per cent of loci (Harris and Hopkinson, 1972) the regional homozygosity becomes

$$.72(1) + .28(.6366) = .8982$$

and local homozygosity is

$$.72(1) + .28(.7024) = .9167$$

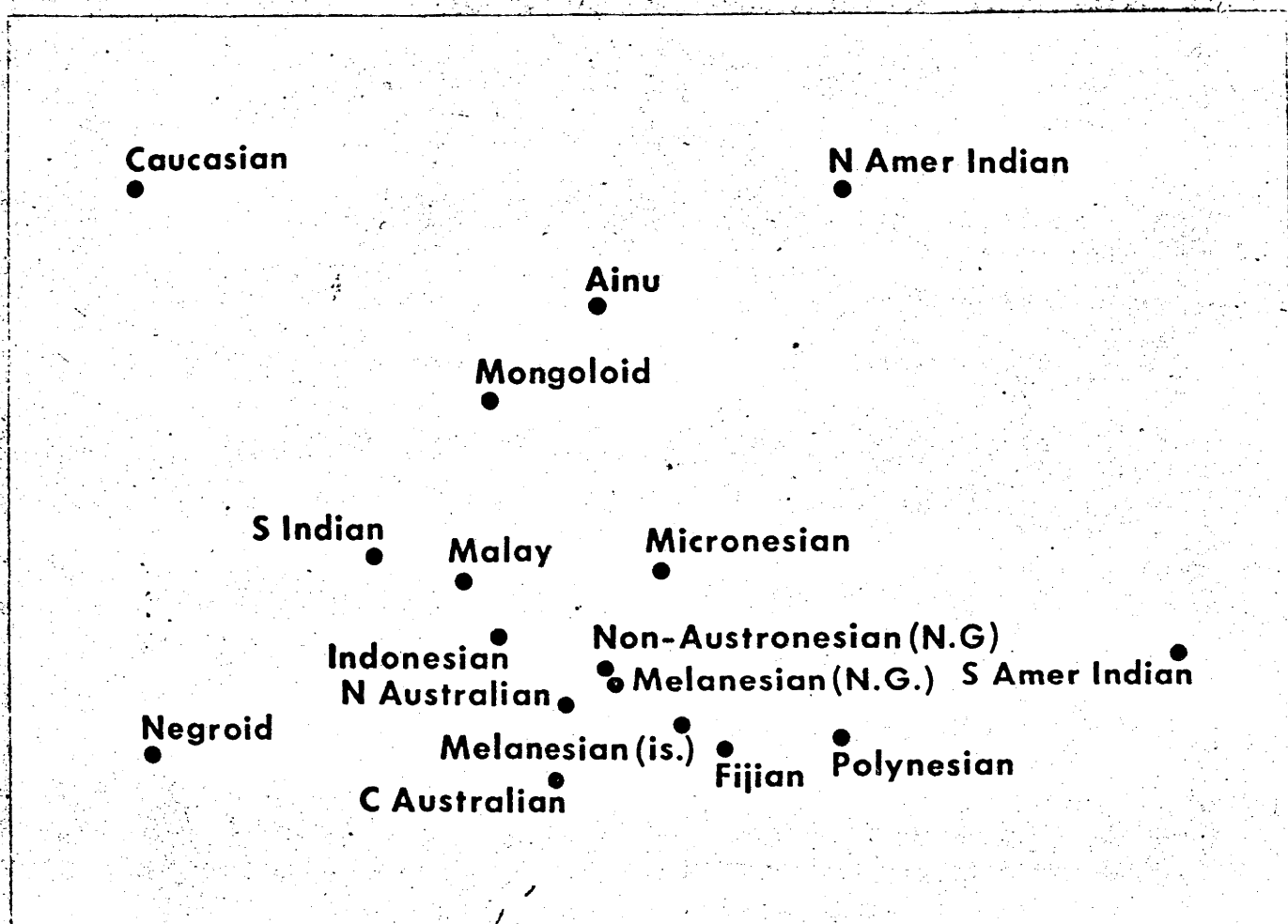


Fig. 3. Geographic locations of the 17 populations

Table 5: Kinship (upper triant) and Hybridity (lower triant) within systems

	N. Aust	C. Aust	NAN	MN (NG)	MN (Is)	Micro	Poly	Ind	Fiji	SA Ind	NA Ind	Neg	Cauc	Mong	Ainu	Malay	S. Ind
N. Australian	.1647	.1402	.0014	-.0186	-.0294	-.0080	-.0973	-.0533	-.0476	.0524	.0062	-.0333	-.0224	-.0033	.0142	-.0643	-.0021
C. Australian	.0188	.1706	-.0227	-.0398	-.0369	-.0103	-.0924	-.0629	-.0438	.0723	.0006	-.0964	.0051	.0113	.0487	-.0692	.0252
Non-Austronesian	.0884	.0983	.1656	.1211	.1197	.0578	.0162	.0646	.0772	-.0875	-.0776	-.1275	-.0732	.0210	-.0760	-.0504	-.0880
Melanesian (N.G.)	.0885	.0957	.0196	.1349	.1270	.0861	.0448	.0724	.0954	-.0697	-.1010	-.1442	-.1199	-.0063	-.1009	-.0076	-.0969
Melanesian (Is.)	.0990	.1000	.0226	-.0080	.1514	.0722	.0758	.0529	.1132	-.0722	-.1048	-.0993	-.1081	-.0233	-.1063	-.0143	-.1178
Micronesian	.0706	.0711	.0376	.0140	.0267	.0879	.0204	.0449	.0694	-.0385	-.0791	-.1074	-.0949	.0046	-.0668	.0187	-.0575
Polynesian	.1316	.1279	.0736	.0462	.0392	.0502	.1486	.0038	.0702	-.0446	-.0737	.0406	.0171	-.0228	-.0713	.0383	-.0660
Indonesian	.0956	.0997	.0368	.0239	.0390	.0240	.0611	.0972	.0588	-.0794	-.0073	-.1206	-.0566	.0157	-.0411	.0392	-.0287
Fijian	.0990	.0955	.0362	.0085	.0121	.0183	.0330	.0262	.1198	-.0761	-.1010	-.0922	-.0975	.0016	-.0847	.0160	-.0793
S. American Indian	.0560	.0434	.1253	.1040	.1115	.0786	.0983	.1014	.1046	.1422	.0537	.0159	.0512	.0124	.0402	-.0261	.0534
Negroid	.0886	.0887	.1328	.1326	.1405	.1097	.1261	.0774	.1304	.0565	.1747	.0584	.0907	.0070	.0683	.0078	.0703
Caucasian	.1073	.1334	.1456	.1434	.1335	.1143	-.0057	.1251	.1208	.0838	.0749	.1742	.0372	-.0669	.0165	.0296	-.0112
Mongoloid	.1029	.0902	.1265	.1374	.1390	.1145	.0903	.0979	.1243	.0618	.0553	-.0004	.1717	-.0055	.1149	-.0250	.1070
Ainu	.0562	.0505	.0632	.0511	.0621	.0295	.0604	.0265	.0404	.0431	.0584	.0885	.0610	.0327	.0156	.0164	.0314
Malay	.0817	.0625	.1252	.1264	.1345	.0991	.1176	.0890	.1154	.0595	.0600	.1061	.0365	.0467	.1592	-.0254	.1274
S. Indian	.1029	.1041	.0926	.0690	.0726	.0390	.0463	.0313	.0490	.0771	.0727	.0666	.0864	.0263	.0821	.0995	.0013
	.0797	.0662	.1206	.1160	.1307	.0860	.1057	.0733	.1034	.0450	.0506	.0937	.0279	.0281	.0131	.0591	.1311

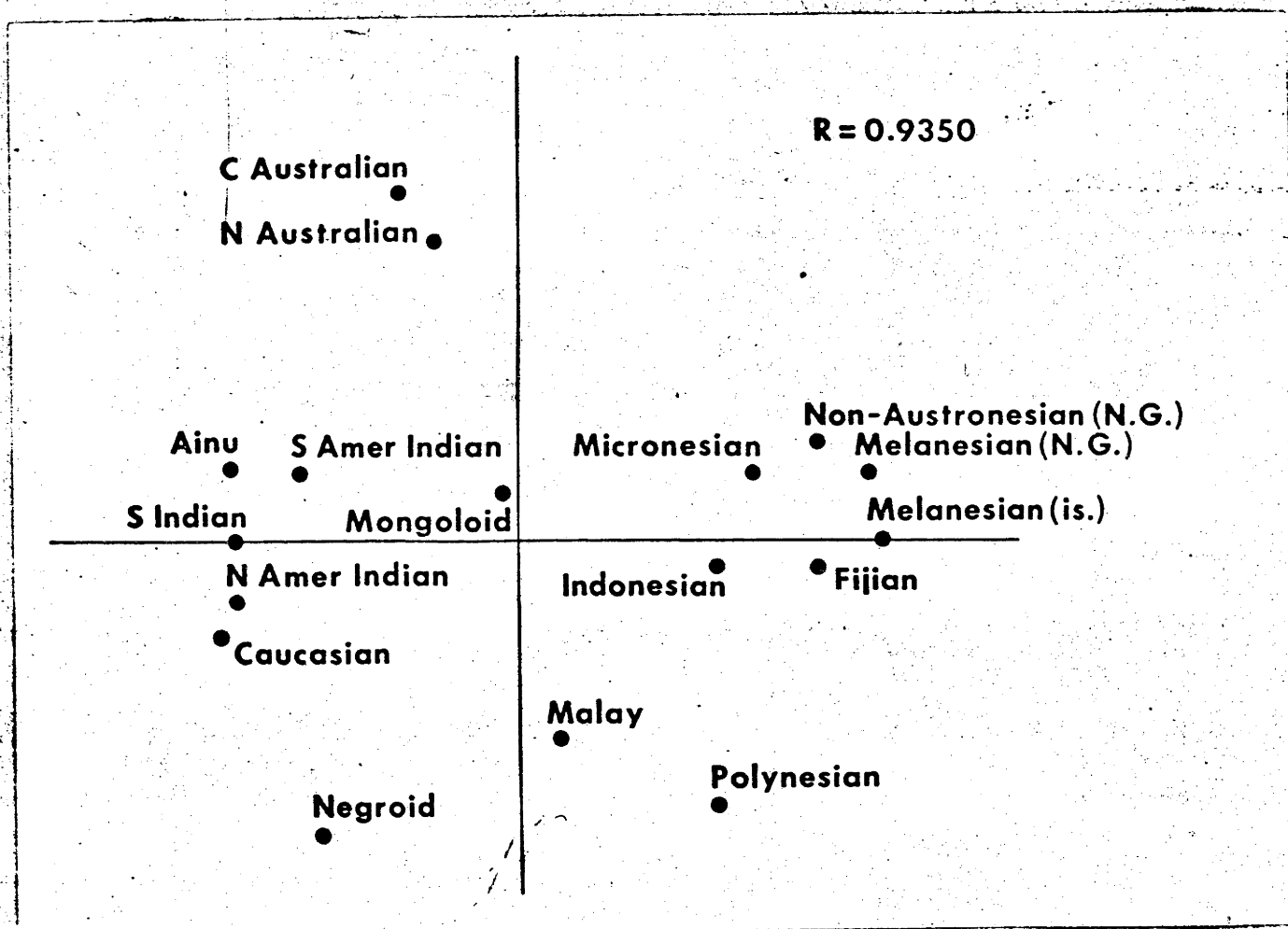


Fig. 4. Principal components of kinship within systems

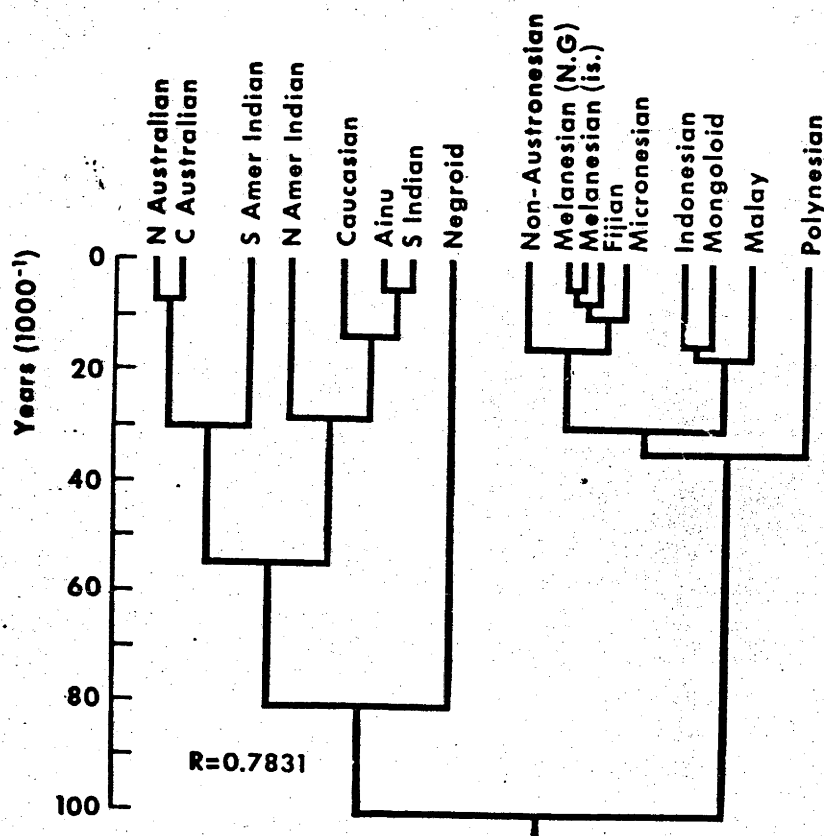


Fig. 5. Cladogram from kinship within systems

Table 6: Parameters of population structure by system

Genetic system	Mean	Mean	Mean	Regional		Local		Malecot parameters		
	kinship ϕ_1	kinship ϕ_2	hybridity 0	homozygosity ΣQ^2	homozygosity Σq^2	a	b	L	(1-L)a+L	
ABO	.0620	.0583	.0319	.5498	.5777	.0644	.0008	-.0098*	.0552	
MNS	.1618	.1610	.0910	.3931	.4913	.2050	.0003	-.0395	.1736	
Rh	.2336	.0971	.0620	.4561	.5832	.1499	.0002	-.0687	.0915	
Inv	.0582	.0582	.0313	.6154	.6378	.0617	.0019	-.0040	.0579	
Fv	.3798	.2572	.1347	.6610	.7898	.2996	.0003	-.0265*	.2810	
K	.0682	.0682	.0406	.9733	.9751	.0728	.0010	-.0059	.0673	
Phs	.1583	.1555	.0921	.6444	.7007	.1738	.0006	-.0199	.1574	
PGD	.0509	.0516	.0281	.8575	.8648	.0608	.0003	-.0116	.0499	
PGM ₁	.0481	.0458	.0246	.6936	.7083	.0588	.0005	-.0082	.0511	
Tf	.0650	.0676	.0411	.9357	.9399	.0830	.0004	-.0111	.0723	
Gc	.0501	.0384	.0206	.6272	.6458	.0401	.0031	.0001*	.0402	
Hp	.1271	.1270	.0694	.5138	.5756	.1501	.0004	-.0262	.1278	
Gm	.4406	.5928	.3269	.3552	.6393	.6362	.0007	-.0695	.6109	
Mean	.1464	.1368	.0765	.6366	.7024	.1582	.0008	-.0231	.1413	
Standard deviation	.1307	.1506	.0824	.1936	.1491	.1621	.0008	.0231	.1569	

* Because of failure of 3-parameter iteration to converge L was taken as mean for other systems or from Imai et al (1973), whichever gave smaller variance.

Kinship among systems remains virtually unchanged at $\cdot 1817$. Thus kinship within a region is much less affected by preferential sampling of polymorphisms than is random homozygosis. The bias noted by Latter (1973) for the more polymorphic loci to give higher estimates of kinship is eliminated by taking means of homozygosis among systems. Our results suggest this bias is not large for human races, and is therefore negligible for local populations. Because estimates of homozygosis are so unstable, we prefer to express population structure in terms of kinship.

In recent years theoretical population genetics has devoted much attention to the controversy between Darwinian advocates of selection and non-Darwinian proponents of neutral mutation (Lewontin, 1973). The question at issue concerns the systematic pressure for a species not undergoing introgressive hybridisation,

$$(11) \quad k \equiv U + pS$$

where U is the mutation rate for neutral and advantageous alleles, and p is the proportion of these that are advantageous, with mean advantage S (Morton, 1973b). We want to know the fraction pS/k of systematic pressure which is selective, an inquiry that may usefully be pursued if, and only if, the selection pressure S is large relative to the mutation rate and the systematic pressure k is measurably great.

Unfortunately, this condition may be met for only a small fraction of loci. Several calculations indicate that the expressed genetic load in man cannot exceed unity, and therefore the typical systematic pressure must be less than 10^{-4} per locus per generation (Morton, 1974). An independent approach takes an amino acid substitution rate of 10^{-9} per year for a gene of 500 codons with a generation time of 20 years, for a systematic pressure of 10^{-5} . If there is synergism, the systematic pressure is even smaller. It may be larger if much selection is in response to transient conditions and does not lead to fixation. However, even if such transient selection is 100 times greater than pressure toward fixation, it is too small to be measured. The great controversy over non-Darwinian evolution is beginning to founder for lack of critical evidence.

These considerations do not preclude generations of intense selection, but they do mean that most loci are nearly neutral most of the time. It seems likely, therefore, that most gene frequency variation in the Western Pacific is neutral. In the remainder, we are unlikely to be able to demonstrate the selective forces involved. This should encourage investigation of any system where special considerations suggest that selection may be important, at the same time that it discourages attempts to find a selective explanation for most gene frequency variation.

We have seen that evolutionary size of populations in the Western Pacific is small. The simplest explanation is that, to a greater extent than in Eurasia, the present day distribution reflects settlement by a small number of founders, with restricted subsequent introgression. This was probably typical of pre-agricultural and swidden man, and of Europe before the Roman empire, and so the Western Pacific is of special interest for study of population structure.

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