# A MORPHOMETRIC STUDY OF CRANIAL SHAPE IN THE HOMINOIDEA

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# ABSTRACT

This study investigates the applicability of a number of traditional and newer methods of morphological description to the problem of defining hominoid cranial form. The aim has been to produce an objective assessment of the relative merits of the methods from both a practical and theoretical perspective.

The thesis is presented in three parts. In the first, several approaches which offer potential in the description of cranial morphology are reviewed and the phenetic relationships of the crania of extant hominoids are examined using data obtained by a variety of new (shape factors, least squares, and Fourier analysis) and more traditional (dimensions, angles and indices) approaches to morphological description. The analysis concentrates on a comparison of the resulting patterns of group dispositions and on an examination of the ability of the various approaches to allow an accurate determination of the affinities of crania of unknown provenance. The results indicate that there is little difference in the patterns of phenetic relationships obtained although it appears that the analyses based upon linear and angular measurements and Fourier coefficients provide the widest separation between the groups.

The second study employs linear and angular measurements and Fourier coefficients in an examination of within-group cranial variability. In general the results lead to similar conclusions about the patterns of sexual dimorphism in extant hominoid crania and the influence of size on cranial morphology. The analyses of Fourier data differ from those of linear and angular measurements, however, in that purely size related variation is given a smaller weighting relative to morphological variation attributable to other sources.

In the third part the fossil record relating to the evolution of *Homo* is reviewed. The third study employs these same two approaches to morphological description in a study of the patterns of cranial variation between certain fossil hominids. By contrast with the first study the pattern of phenetic relationships between OTUs appears to be considerably influenced by the choice of measurement method although there is a common underlying pattern of group dispositions. The reasons for these differences are considered in the light of the results of multivariate morphometric studies of cranial form undertaken by other workers.

From these studies it is concluded that:

a) the results obtained by studies employing landmark dependent and data with reduced landmark dependence may differ to some degree and that this difference is principally related to differences in the ways in which the various anatomical regions influence the measurements,

b) the choice of method for craniometric problems should be determined with due regard for the task at hand,

c) the investigator should be aware of the potential pitfalls and advantages of each method in furnishing answers to specific questions,

d) the investigator should be aware of the fact that the use of different morphological descriptions may give rise to different results.

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# ABBREVIATIONS

| | |
|---|---|
| a.m. | Anatomically modern |
| B.P. | Before present |
| CA | Canonical Axis |
| DNA | Deoxyribonucleic Acid |
| m.y. | Millions of years |
| SDU | Standard Deviation Units |
| t.y/k.y | Thousands of years |
| PC | Principal Components |
| PCA | Principal Components Analysis |
| UPGMA | Unweighted Pair Group Method using Averages |

# CHAPTER 1

## Cranial form in the Hominoidea

## – a general introduction

## General Introduction

The work described in this thesis was begun and inspired by the late Professor E.H. Ashton of Birmingham University and follows the same biometric tradition which was enthusiastically developed over a number of years by Professor Ashton, his students and co-workers.

## Objectives

This study investigates the applicability of a number of methods of morphological description to the problem of defining hominoid cranial form. The aim has been to produce an objective assessment of the relative merits of the methods from both a practical and theoretical perspective.

## Context

By far the commonest approach to the quantitative description of biological forms relies upon the identification of landmarks. Traditional craniometry is no exception to the general rule in that it involves the use of a great number of easily recognisable and precisely defined landmarks (see for example Martin, 1929, Howells, 1936, Trevor, 1950). It suffers, however, from a number of significant problems.

First, the description of cranial morphology by the use of linear and angular dimensions is bound to be influenced by the distribution and density of the standard craniometric landmarks. Regions such as the face and cranial

base offer a large number of readily definable and identifiable prominences and sutural junctions. By contrast, the vault and other regions in which bones are smoothly curved and the number of sutural meeting places is limited (which may make up a considerable proportion of the skull) offer relatively few landmarks. In consequence, traditional craniometric descriptions may fail to adequately describe "whole" morphology since the regions between landmarks are unsampled.

Second, the standard approach to craniometry results in a set of measurements which are relatively disconnected and do not describe morphology in a systematic way. As a result some measurements may, to a degree, simply repeat information contained in others and it is not possible to know what proportion of the available information is described by any given set of measurements.

Other problems, not necessarily peculiar to standard craniometry, include the difficulty of ensuring repeatability of observations between observers, the time and effort required to collect and encode the data and the difficulties associated with ensuring equivalence of landmarks between crania from different species.

Recent developments (e.g. the work of Lu, 1965, Sneath, 1967, Rohlf and Archie, 1984 and others) have suggested that the traditional biometry based upon dimensions taken between landmarks may be superseded by a new biometry. These new developments include refinements of landmark based techniques so that the resultant data include information relating to the curvature of regions between landmarks (see Bookstein, 1977a, 1978) and

methods which may allow the description of cranial form with a reduced dependence on the need to define landmarks (see Lestrel, 1974, 1978). Some of the methods with a reduced dependence on landmarks offer potential for determining the proportion of total morphology which is described and for the automation of data collection and encoding.

As yet, however, there has been little effort devoted to comparing the newer methods with each other and with more traditional approaches. Consequently the relative merits of the methods and the effects of using different approaches to shape description on observed phenetic relationships between crania are largely unknown.

## Structure of this thesis

The work described in this thesis tests the hypothesis that the pattern of phenetic relationships observed between crania is independent of the method used to describe morphology.

In addition attention is paid to differences in:

a) the extent to which different methods allow the accurate identification of crania of unknown provenance,

b) the interpretability of the generated data and of the observed phenetic relationships of crania,

c) the practical aspects of the use of the methods.

The thesis is presented in three parts:

In the first a number of approaches which offer potential in the description of cranial morphology are considered. This is followed by a phenetic study in which some of these methods are applied to the description of cranial form in extant hominoids with the aim of allowing a preliminary appraisal of their relative merits.

The second part builds upon the findings of the first by comparing the patterns of within-group variation of cranial form in extant hominoids which emerge from analyses using the apparently two most effective craniometric approaches.

The third part of the thesis once again compares these two methods – this time in a situation where the between-group differences in cranial

morphology are less extreme than those in the first part of the study. The material used consists of the crania of a number of extant and fossil hominoids.

# Chapter 2

# A consideration of the available methods for the description of cranial form

## INTRODUCTION

Recent developments in computing and in the technology of image processing have made available a number of methods for the description of the form of irregular objects. Some of the newer approaches describe form without the need to define landmarks, consequently comparisons between objects can be made without the need to identify homologies. Potentially, these methods can be applied to the description of cranial morphology. They may offer some advantages in that an exhaustive mathematical description of even the most irregular or smooth, landmark free, objects is now possible.

Despite recent efforts to apply some of these methods in a number of contexts (e.g. Lestrel, 1974, 1982, Rohlf and Archie, 1984, Yasui, 1986, Johnson *et al.*, 1985) little information regarding their relative practical and theoretical merits is available. As a consequence it is unclear whether one method is of more use than another in a given circumstance.

It is the purpose of this, the first study to be described in this thesis to consider the applicability, practicality and efficacy of a number of methods in the description of cranial form in the Hominoidea. To this end the chapter begins with a consideration of methods which are available for the description of the morphology of biological structures. Methods which are dependent and those which are independent or have a reduced dependency on the definition of homologous landmarks are described and their theoretical advantages and disadvantages considered.

This preliminary review is followed by a study which is directed to a consideration of the practical benefits and disadvantages of each approach to morphological description. The study aims to compare the phenetic relationships of the crania of living hominoids as implied by studies using traditional craniometric approaches (dimensions angles and indices) with the phenetic relationships implied by newer approaches (Sneath's (1967) distance $-D_h$, Shape factors and Fourier analysis). This study investigates the following questions:

a) To what degree do the phenetic relationships between living hominoid crania differ when midline data are studied instead of data from midline and off-midline structures? It is important to know this because the newer methods of shape description are, at present, limited for practical purposes to midline tracings. Improvements in technology will probably remove this limitation in due course.

b) To what degree do the phenetic relationships between living hominoid crania differ when the crania have been described by methods which have a reduced or no dependency on the definition of homologous landmarks? To this end the phenetic relationships of crania which are implied by the studies of a) (above) are compared with those implied by newer methods.

c) More generally, considering the findings of a) and b) which methods appear to offer most potential in adequately describing and in allowing suitable statistical comparisons of hominoid cranial morphology?

In the studies to be described in this chapter the hypothesis which is consistently explored is that there are no differences in the results of phenetic studies which use data collected by the means described above.

# A REVIEW OF METHODS WHICH OFFER POTENTIAL IN THE DESCRIPTION OF CRANIAL SHAPE

## I. "Homology" dependent methods of shape description

By far, the commonest approach to the quantitative definition of biological form has been the use of measurements taken between defined morphological landmarks.

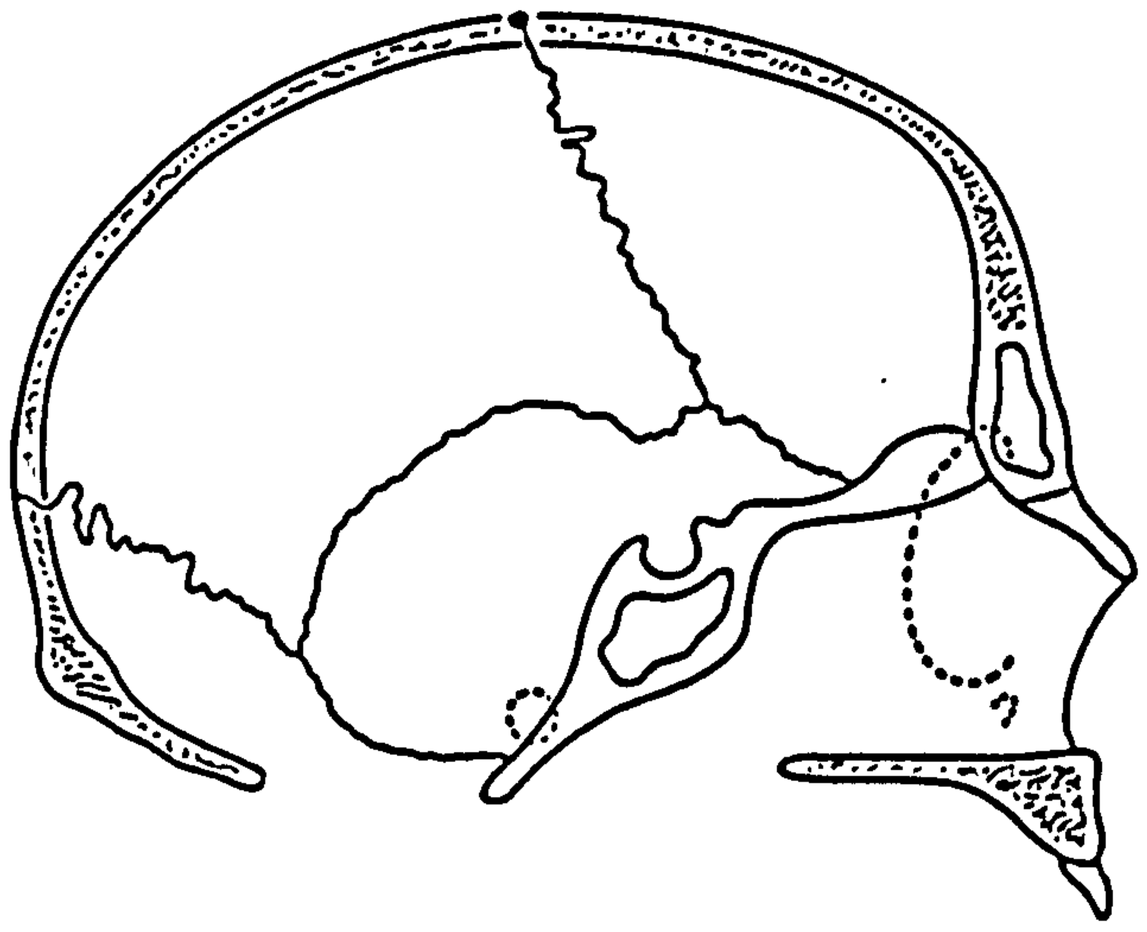
A landmark is an identifiable point on the form which is to be described. In order to compare forms, it is essential that the landmarks used in the comparison are in some sense equivalent. In studies of biological forms, the equivalence which is usually implied is biological (i.e., ontogenetic or phylogenetic).

In practice, landmarks may be of three kinds viz. tips of prominences, extremal points (e.g. the most dorsal), or features located within the outline (e.g. sutural junctions). It is possible, however, that features located within outlines may vary between forms with similar shapes (figure 2.1) and they should be used with caution.

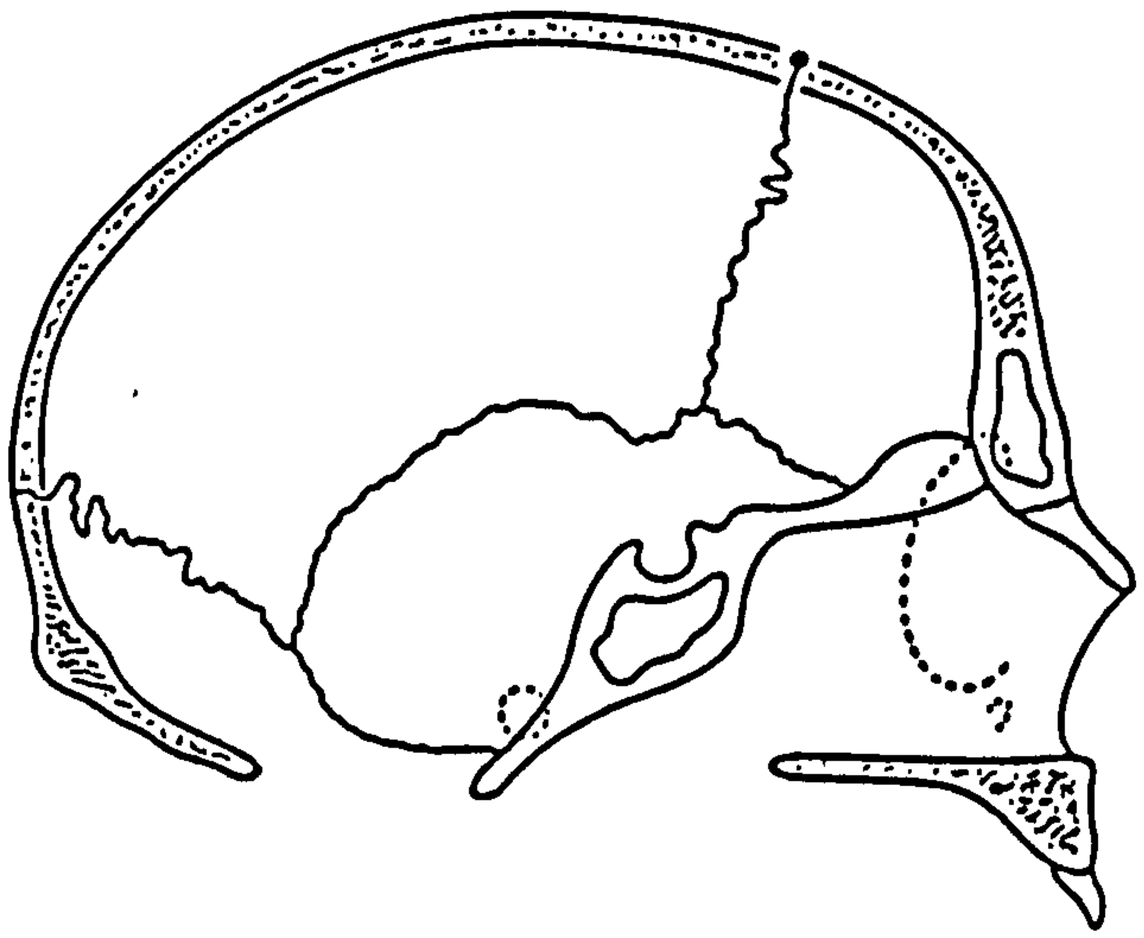
The use of data taken between landmarks for comparing forms has a long history in biology. Measurements are taken from populations and compared either singly or simultaneously by means of multivariate statistical analysis.

The comparison of measurements taken between homologous landmarks on two forms is primarily directed towards the study of shifts in homologies as a result of evolution, growth, or some other factor. Mathematical shape difference is related to homology shift.

FIGURE 2.1 – Features located within outlines may vary between forms with similar shapes. Compare the position of bregma in a, with that in b.



a



b

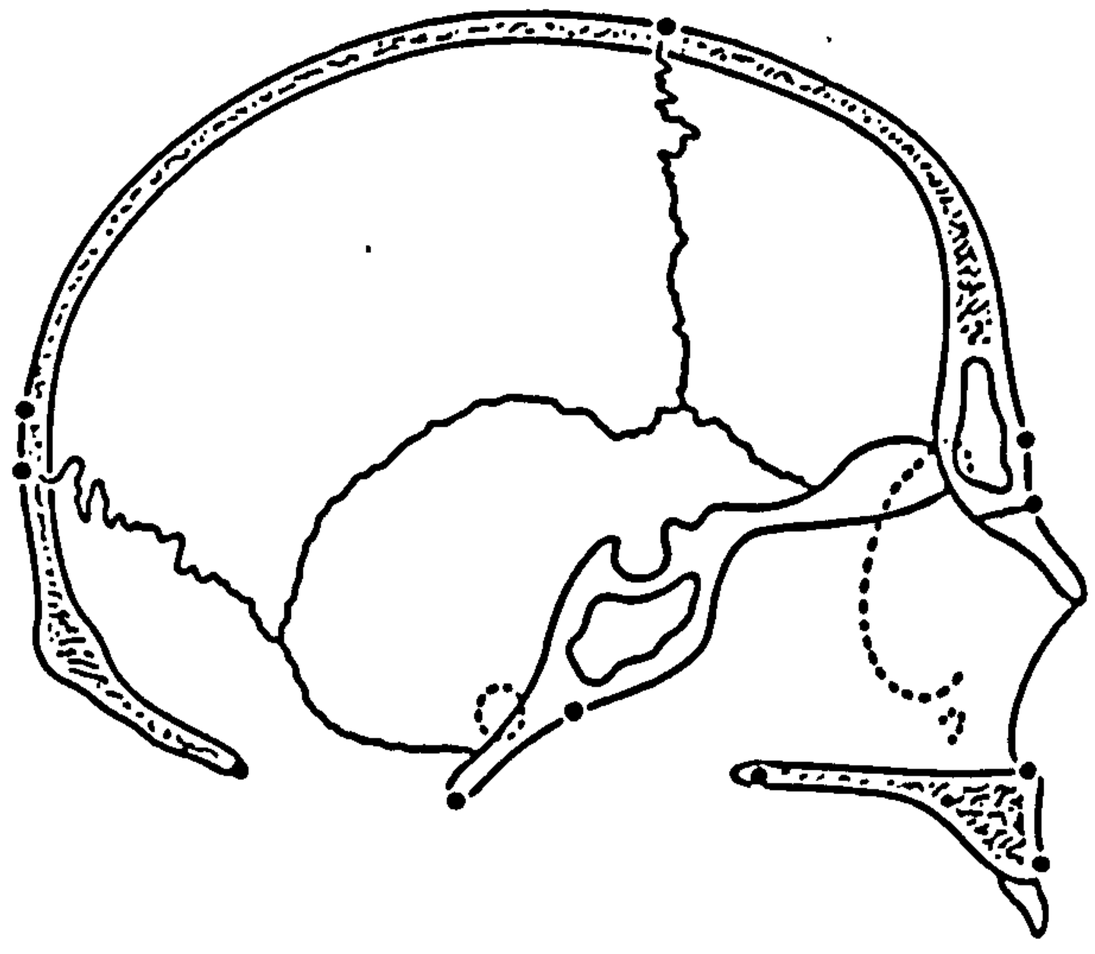
Fig 2.1

In practice, biological materials differ in overall shape by relative shifts and changes in the size and shape of homologous regions and do so in highly complex ways. It seems unlikely that the study of comparative data taken between a set of homologous landmarks on organisms or parts of organisms is the optimal way to answer questions about "pure" shape differences: rather it is an appropriate way to answer questions about differences in the positions of postulated homologies.

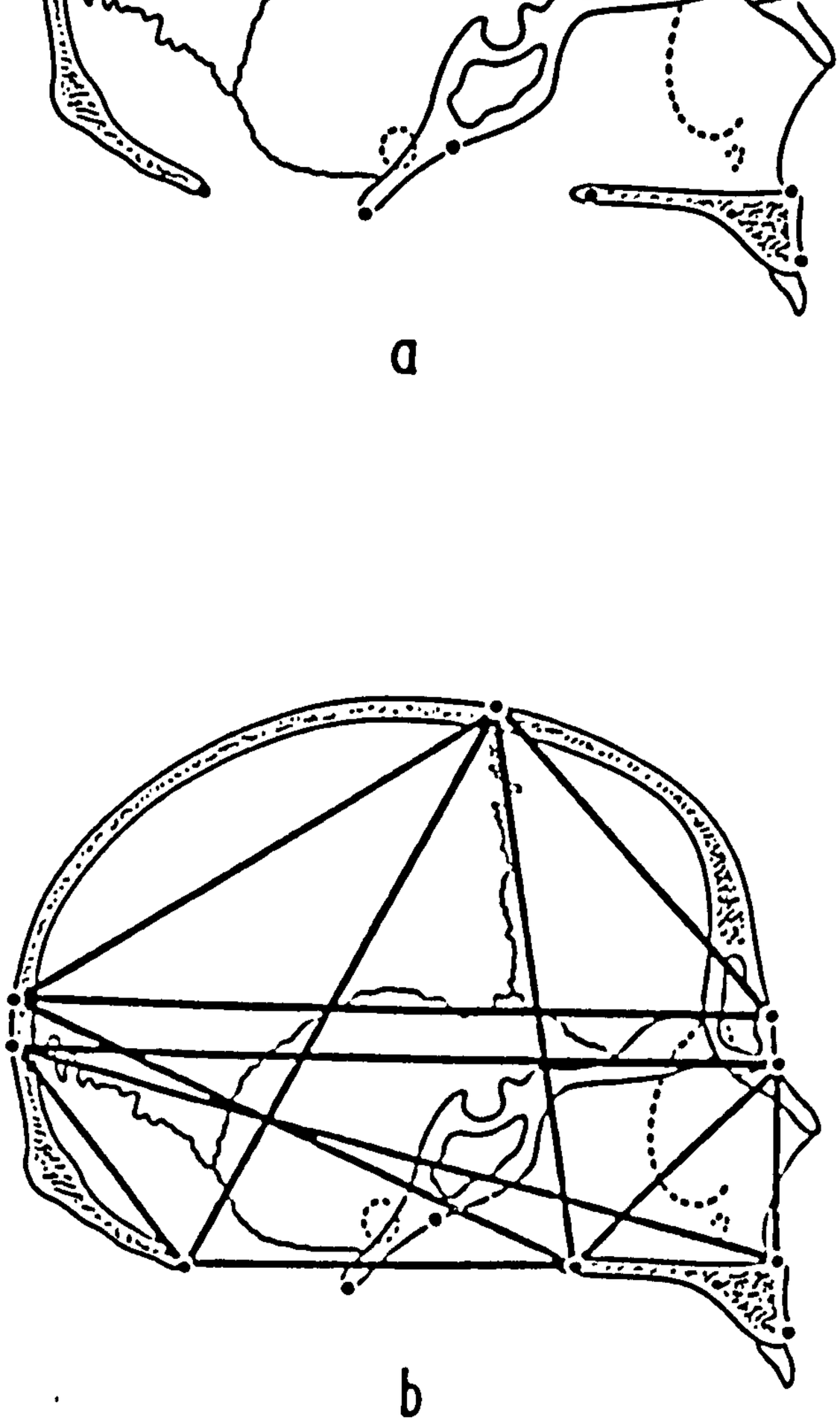
A criticism which can be levelled against the way in which landmark data are commonly collected, at least in anthropology, is that they are taken almost randomly. No attempt is made to describe systematically the relative location of landmarks, one to another. Measurements are taken in the hope that their multivariate compound will sort out the organisms in some form related way. The difficulties encountered in defining form by landmarks are illustrated in figure 2.2.

More recently increasing use has been made of Cartesian co-ordinate data for describing cranial morphology (eg. Creel & Preuschoft, 1976). These co-ordinates, which are frequently three-dimensional, allow a relatively complete description of cranial morphology in which landmarks can be easily related one to another. Corruccini (1988) has investigated the differences obtained in the results from studies using cartesian co-ordinate data and those using linear dimensions taken from the same landmarks. His study indicates that "much similarity is found between analyses using input data in the form of chords and co-ordinates. The subtle differences attain statistical significance, however, with the greater interspecific separation and delineation of trends consistently favouring chords" in a study of primate odontometrics and co-ordinates in a study of pelvic morphology.

FIGURE 2.2 – Measurements taken between the landmarks in a) will only incompletely describe the Morphology of the cranium (b). Some areas, especially the vault are very poorly described.



a



b

Fig 2.2

The distances between landmarks are influenced by the size as well as the shape of organisms. A common manoeuvre intended to eliminate the effects of size on a set of data is to re-express each variable as a ratio (variable/size variable). This manipulation does not render data independent of size. A full discussion of the problems associated with the use of ratios is given by Atchley *et al.*, (1976) and further considerations are furnished by Albrecht (1978a). The essence of the argument is that the ratio, Y, made up of a "nonsize" variable $x_1$ and a "size" variable $x_2$;

$$Y = x_1/x_2$$

will be related to the size variable, Z, ($Z=x_2$). In a typical data set, Y will be correlated with Z. This correlation will vary as a function of the correlation between $x_1$ and $x_2$ and of the ratio of the coefficients of variation for the two original variables. The underlying distribution and structure of the data are altered.

The comparison of measurements taken between landmarks on two forms is primarily directed towards study of shifts in their disposition. Sneath (1967), has described an interesting variant on the traditional approach. Instead of measuring the distances between landmarks and using these to examine "shifts" in the "homology map" he compares the disposition of landmarks (as described by their Cartesian co-ordinates) between specimens. The comparison is effected in two stages, first the "spread" of landmarks is equalised between specimens, this makes their "sizes" the same. Second the diagrams are located "on top" of each other and are rotated with respect to each other. The sum of squared distances between

equivalent points on each is calculated at every step of the rotation and the minimum is taken to reflect the "difference" between diagrams. The context in which this measure of "fit" is described is not entirely taxonomic. Sneath continues in the same paper to develop a technique for describing shape change after the manner of D'Arcy Thompson (1961) (see a review of this field by Bookstein, 1986) by representing the "transformation" as the distortion of a rectangular grid. This part of the work is not directly relevant to the task of identifying phenetic groups though the "fit coefficient" is.

A fuller description of this approach will be given later, it is more akin to the statistical comparison of descriptions of organisms than to the description of individuals *per se.* Sneath's description of individual OTU's is simply, the x and y co-ordinates of landmarks.

It is clear that measurements taken between landmarks may provide useful classifications but to assume that these classifications are based on "shape" may be erroneous. In fact, the equivalence classes are created of individuals with similar dispositions of landmarks, the definition of which may or may not be "shape" dependent. Furthermore sampling of form between landmarks may leave considerable areas unmeasured (see fig. 2.2). The comparison of "homologous" dimensions (between "homologous points") is a good way of describing changes in the "homology map" rather than "shape" in a mathematical sense (see later).

The use of landmarks offers the biologist one significant advantage over methods which have a reduced dependence on homology definition, in that they allow questions about regional differences to be posed. It would be impossible to consider differences in the facial skeleton between two apes unless the location of the face relative to rest of the skull were defined on each.

There are, however, several disadvantages or problems associated with the use of landmarks. Some of these are practical and in evolutionary studies at least there is a major philosophical problem. Practical problems in the use of landmarks include the difficulty of defining those based on maximal curvature (observers may disagree on the location of the maximum and the degree of disagreement will in general be related to the rate of change of curvature in a region; the development of digital image technology offers, at least in two dimensional forms, the possibility of automated curvature analysis with consequent improved identification); the lack in some regions of clearly definable points (e.g., the cranial vault) so that landmark based data may give only an incomplete description of such regions; and the fact that, in general, the collection of landmark based data is time consuming.

In evolutionary studies there is a philosophical problem associated with the use of "homologous" landmarks. The problem is that in order to "get started" the identification of homologies requires a pre-existing (evolution orientated) classification. Homologies can only be called homologies in this context if they are known to have the same phylogenetic origin. This "homology problem" is discussed by Sneath and Sokal (1973). The practical approach relies upon the identification of operational homologies (=postulated homology, = isology). The work of Jardine (1969) and Jardine and Jardine (1976) on probablistic concepts of homology is of particular interest in this context.

One way round these problems is to attempt a purely mathematical comparison between forms with no isologous points being defined. Sneath and Sokal (1973) suggest some variant of a least squares fit of data in which outlines are represented by closely spaced points. Scaling and overlapping of forms on

their centroids, followed by rotation to obtain a minimum residual between outlines would, on the whole, group similar organisms together. Convergence, however, seems to be a problem, since convergent forms are, by definition, similar in shape. This consideration aside, there may well be a place in the early stages of construction of phenetic classifications for purely mathematical approaches to shape measurement which are independent of the need to define homologies.

## II. The description of biological form without landmarks

This discussion will be directed primarily to the relatively simple task of two dimensional shape analysis. The methods of quantification are extensible, at least in theory, to studies of solid, three dimensional objects but the current state of the art makes this impractical, the task of obtaining comprehensive three dimensional co-ordinates, and of handling the required computations being the limiting factors.

The first problem in attempting a study of two dimensional outline data concerns the means of projecting three dimensional objects into two dimensions. Frequently some means of standardisation on recognised planes (e.g. median) is required: there have been two approaches to this. The first is illustrated by the work of Yasui (1986) who manually projected points from human crania onto a plane parallel to the median plane of each. An alternative is to photograph each object under study in a standard orientation and then to treat the photographs as projections of the forms (e.g. O'Higgins and Williams, 1987).

The outlines of such projections can be manually measured, though quantities such as area or perimeter present problems. The planimeter has nowadays been replaced by a digitising tablet attached to a computer. Points are sequentially read from the outline at frequent intervals and stored as a series of x,y co-ordinates. The task is time consuming and prone to operator error. Computer vision systems which collect whole images and allow their manipulation, pixel by pixel have recently become available. It is relatively simple to extract from such systems outline co-ordinates read directly from an object. Details of such an apparatus are given in Johnson *et al.* (1985).

Outlines which are recorded in the form of Cartesian co-ordinate data cannot be directly compared: the co-ordinates differ in value because of differences in position and orientation of objects as well as differences in size and shape. If measurements are to be taken from outlines in a way that will allow comparison they have to be invariant to rotation and translation or they need to be referred to the outline itself. For the comparison of two dimensional objects two reference points defined on each are needed. One point serves to fix relative position and the second relative orientation. An example of such a system is furnished by the manoeuvre of converting Cartesian to polar co-ordinates (e.g. Yasui, 1986).

Some means of two dimensional shape analysis are invariant to rotation and translation and to differences in area enclosed by an outline, whilst others may exhibit a more limited invariance.

"Shape factors"

Under this heading I shall describe a series of shape descriptors which are invariant to differences in position and orientation of the object under measurement. They are very simple to derive computationally and require only basic data about each shape. "Shape factors" are invariably ratios and as such should be used subject to the cautions of Atchley *et al.* (1976). Examples of their use in biology are furnished by studies of cell shape (e.g. Young, Walker, and Bowie, 1974) and of cranial form in the primates (e.g. Ashton, 1981)

The simplest "shape factor" of all is the ratio;

max. length / max. breadth at 90° to max. length

this measure will reflect "elongation" of the shape in a relatively poor way. Only four outline points are sampled and many different "shapes" will share the same numerical value. For shapes with many undulations, maximum projections at 90° can be used.

More computationally complex measures compare such things as the perimeter of an outline and the area enclosed by it. Exner (1978) has described several such measures, e.g.;

$$f_1 = 4.\pi.\ A \ / \ P^2$$

$$f_2 = P - \sqrt{P^2 - 4.\pi.A} \ / \ P + \sqrt{P^2 - 4.\pi.A}$$

where;

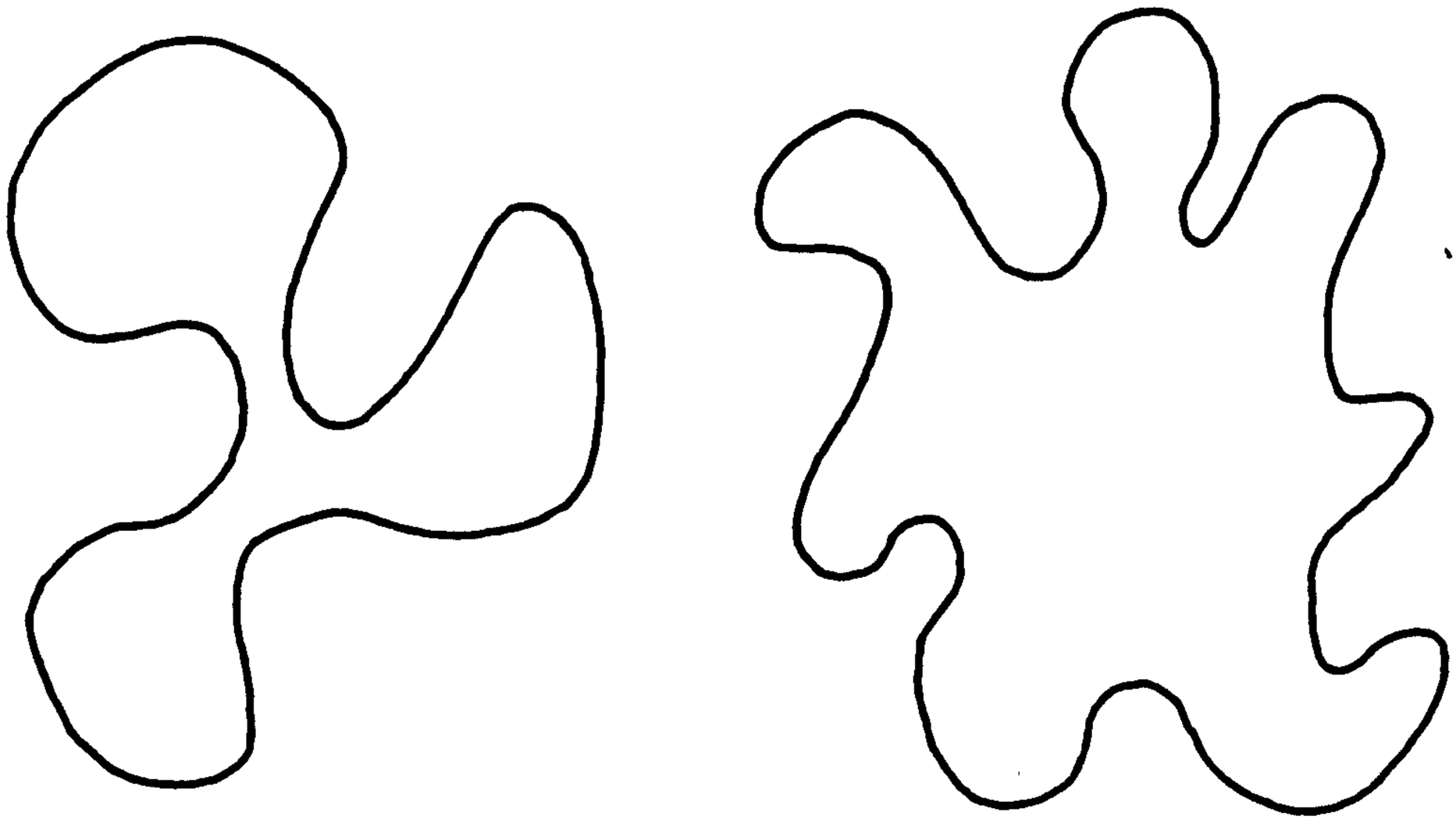
A = enclosed area, and P = perimeter

For a circle:

$$P^2 = 4.\pi.A$$

so $f_1$ and $f_2$ will be equal to unity. As the ratio A / P varies so will each "shape factor". Shapes with undulating outlines will have small values of each factor relative to more "circular" shapes. Outlines which look quite different can have similar values of one of these simple measures (fig. 2.3). Several different shape factors may be simultaneously considered in order to more clearly define form.

FIGURE 23 – Two outlines which are quite different may have very similar values of F1




$$f_1 = \frac{4.\pi.A}{P^2}$$

Fig 23

## Bending energy

An interesting and potentially useful shape measure has been described by Young, Walker and Bowie (1974). They point out several problems associated with the measures described above which include lack of robusticity and the possibility that some of their properties may be altered in the transition from analysis of shapes on a continuous surface to the analysis on a discrete grid, as is the case in computer image processing. The latter objection seems unlikely to be a cause of significant error and there are computational ways of minimising this, but the former is more serious.

The measure described by these workers is based upon the notion of "bending energy". They point out that a two dimensional outline made out of an homogeneous material, if allowed to adopt its "free" form would assume the shape of a circle. This is because a circle is the shape which minimises the stored energy. To make more convoluted outlines requires the expenditure of work in the form of bending energy. The measure they describe creates equivalence classes of figures with equal "stored energy".

The calculation is simple. The shape is divided into small regions;

for a region, n

$$\text{The curvature } K_n = \frac{\text{change in direction in that region}}{\text{length of the region}}$$

The total "bending energy" is given by the sum of $K_n^2$ 's over the whole outline.

This measure is invariant to position and rotation but is affected by size as well as shape differences. This fits in with the intuitive feeling that it takes more energy to bend a short length of material into a circle than a long one.

## Moments

The methods so far discussed have concentrated on the analysis of outlines. Sometimes a form may be specified as a collection of interior points. In the case of digitised images these interior points are the positions of pixels. The calculation of moments treats the distribution of pixels on the x and y axes in a statistical way. This distribution is characterised by having a mean, variance, covariance etc. (see Fisher, 1958, and Moode and Graybill, 1963).

In the field of digital image processing the calculation of moments has proved of value in describing plane images. For a single variable, e.g. the x locations of pixels, $m_p$, the pth moment of x is given by;

$$m_p = \Sigma(x^p) = \int_{-\infty}^{\infty} x^p f(x)dx \quad \text{(Moode and Graybill, 1963)}$$

Thus the zero order moment is the number of points enclosed by the outline.

For a two dimensional distribution, along arbitrary axes x and y the moment of the order (p+q) is defined by;

$$m_{pq} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} x^p y^q f(x,y)dx\ dy \quad \text{(Moode and Graybill, 1963)}$$

More simply;

$$m_{00}=n,\ m_{10}=\Sigma x,\ m_{01}=\Sigma y,\ m_{20}=\Sigma x^2\ ,\ m_{11}=\Sigma x,y,\ m_{02}=\Sigma y^2\ ,\quad \text{etc.}$$

As described the moments are dependent on position and orientation and are thus of little use in taking measures of shape which will allow comparisons between forms differing in registration. Hu (1962) has described two dimensional moment invariants, which are in general more useful in the context of shape comparison. A full description of the use of moments in digital image processing is given by Gonzalez and Wintz (1977).

Dunn and Brown (1986) have applied the method of moments to the study of chick heart fibroblasts grown on grooved substrata. They studied both differences in cell shape and in cell alignment in response to variations in the substrata. Regression analyses were performed to determine the influence of particular substratal parameters such as groove width, and spacing on the moments.

Though well known in digital image processing, moments have been little applied to the study of biological forms. Despite this their use appears promising in situations where landmarks are undefinable or undesirable.

## Medial axis transforms

A very different approach to describing shapes has been developed by Blum (1973). Rather than by a description of the outline, the shape is defined by a medial axis or skeleton and a function. Together these may be called the skeletal pair. Oxnard (1984) has discussed the method and illustrated the medial axis of the projected silhouette of a pelvis (fig. 2.4). Bookstein (1977) describes the principle of operation of this method. He gives several definitions of the "skeleton" of a form. The most concise is "The skeleton is the locus of all points which do not have a unique nearest boundary point upon the shape; the function is the distance to any of the set of equally distant nearest boundary points". The "grassfire model" makes comprehension easier. The shape is characterised as an area of dry grass. If it is fired simultaneously all around the edge it will burn towards the interior. If we assume even rate of burning, the points at which the fire meets itself comprise the points defining the skeleton, the time taken to reach these points is the function.

The skeletal pair will allow a complete reconstruction of the shape, which means that it exhaustively describes it. The skeletal pair is defined by the shape itself; no requirement is placed upon landmark definition. It has been proposed (Bookstein, 1977) that this skeletal pair might form a basis for shape comparison.

The method is commonly applied to problems of character recognition in image processing. In biology it has been applied by Webber and Blum (1979) to the analysis of the form of human mandibles.

FIGURE 2.4 – The stages in the production of a medial axis transform of a pelic silhouette (after Oxnard 1984)

Fig 2.4

## Curvature of outlines

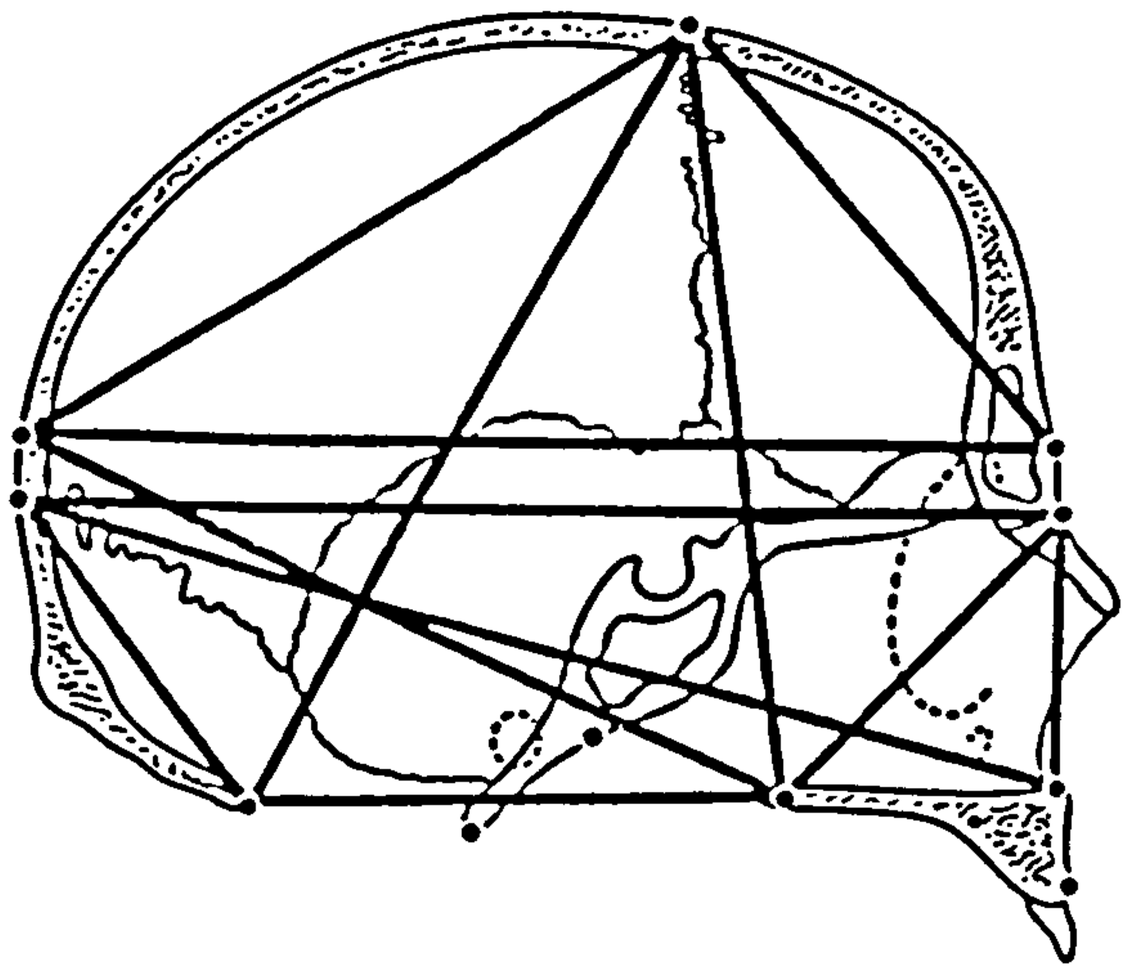
A most promising approach to the study of biological forms would seem to be one based upon a comparison of curvatures around an outline. We have already noted that in many situations biological homologies are defined as "equivalent" (in a relational sense) areas of high curvature in an outline. An example is the inion, the most prominent point on the external occipital protruberence in the mid line of a cranium. A curvature description of an outline might therefore allow automatic recognition of prominences, and reduce subjectivity in the imposition of a point upon them.

Bookstein (1978) has criticised conventional cephalometrics because it obscures the continuous variation of form between landmarks (fig. 2.5(a)). His proposal is to describe the continuous curvature at sample points on the outline (fig. 2.5(b)). The outline can be considered to be a continuous curve. Implicit in the function describing this curve are the actual Euclidian locations of any sample points that are required (each sample point can be described by its tangent angle and arc–length from an arbitrary start point).

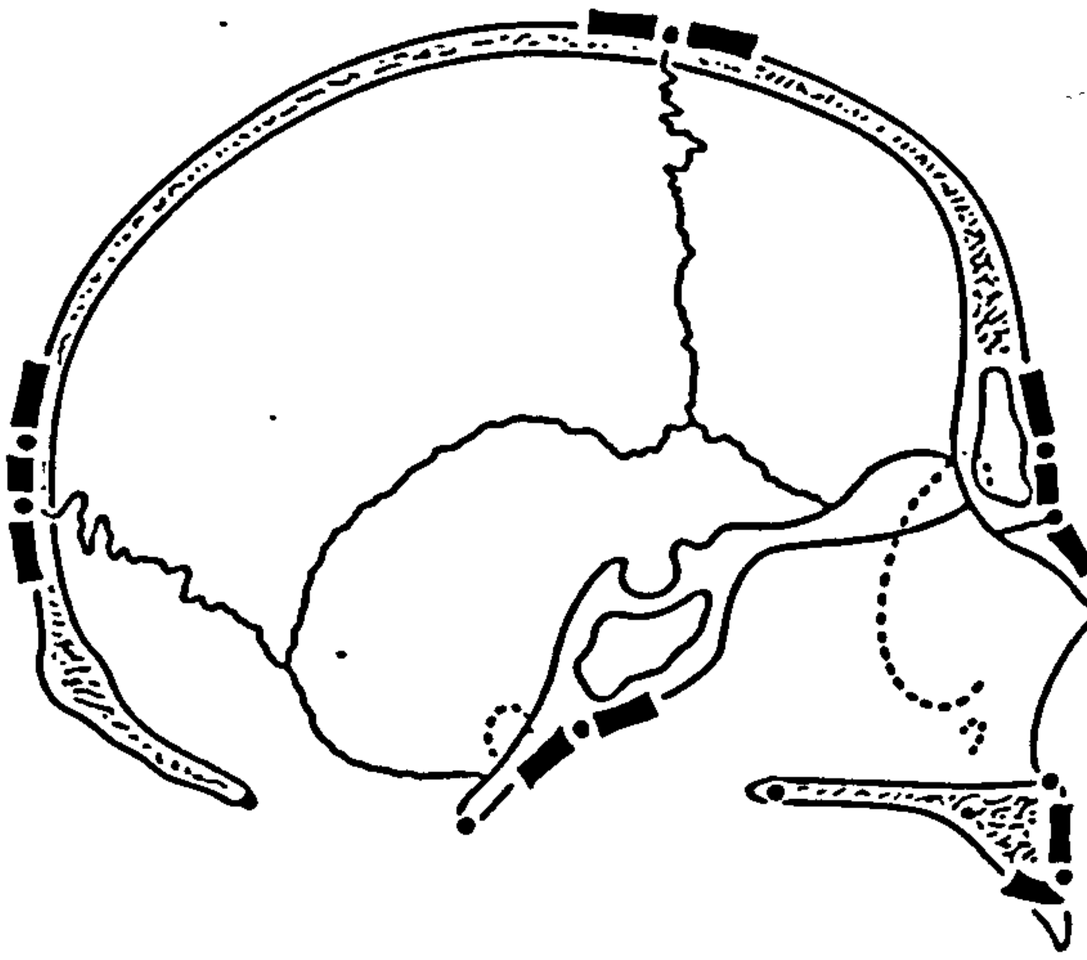
The local curvature at any point on the outline of a shape can be calculated from the chain code (directions from pixel to pixel) of an outline by the means described by Young, Walker and Bowie (1974). By repeated averaging of adjacent curvatures a smooth graph can be drawn.

Another way of describing the curving of outlines is to examine the change in tangent angle with distance around an outline. Rohlf and Archie (1984) describe the application of such an approach to outlines of mosquito wings. Their tangent

FIGURE 2.5 – Conventional cephalometrics (a) obscures the continuous variation of form between landmarks. Bookstein (1978) has proposed the scheme in (b) in which the curvature at sample points is recorded.



a



b

Fig 2.5

angle function is taken from Zahn and Roskies (1972). For equally spaced points around an outline scaled to length 2 $\pi$ they calculate the tangent angle function $\phi(t)$ from;

$$\phi(t) = \theta(t) - \theta(0) - t$$

where $\phi(t)$ is the angle of a tangent vector at a distance t from the start point (tangent here = $\theta(0)$, see fig. 2.6).

FIGURE 2.6 – The tangent angle function after Rohlf and Archie (1984). $\Theta_o$ = angle of the tangent vector at the start point. $\Theta_t$ = angle of the tangent vector at distance t from the start point.

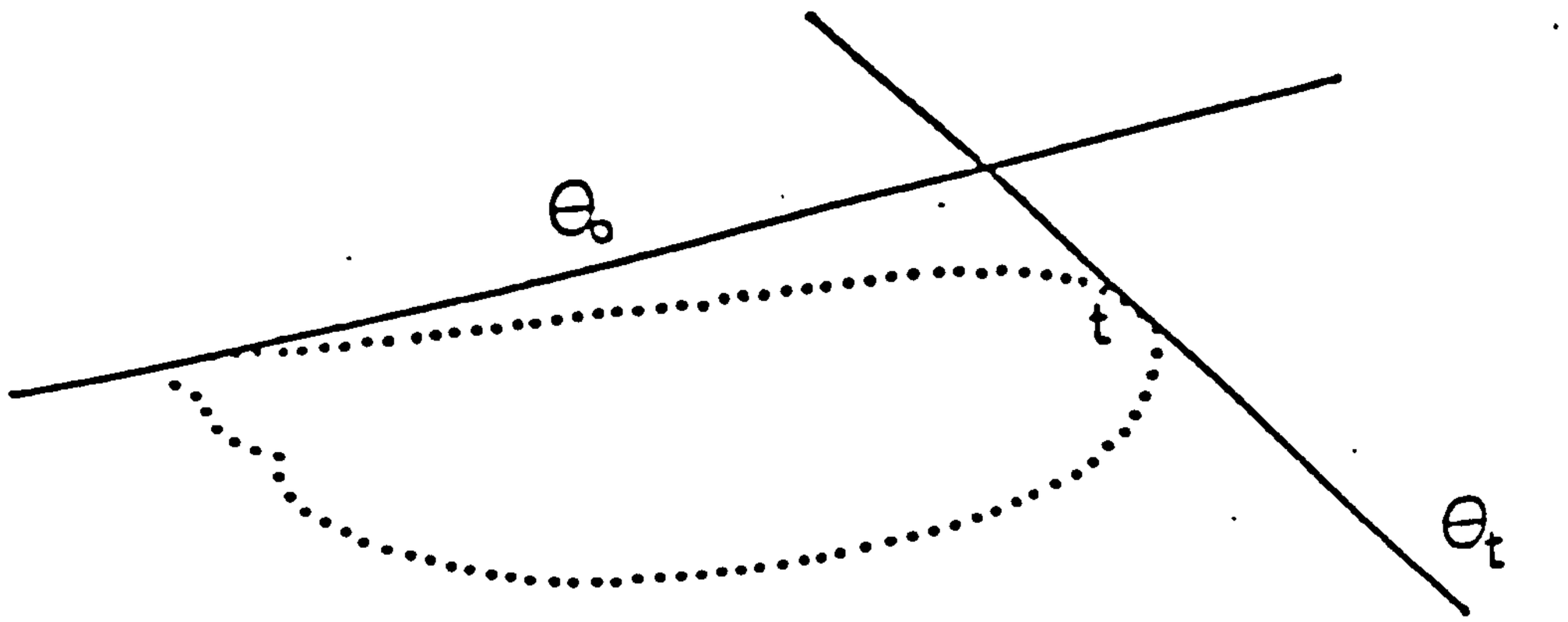



Fig 2.6

Curvature descriptions of outlines "capture" and "preserve" the details that elude simple measures of shape. They have potential in the study of symmetry of outline features. A simple way to examine axial symmetry would be to examine local curvatures regularly spaced around an outline. Starting at a point where the axis of symmetry "touches" the outline, the sum of squared differences in curvatures traced half way round the outline clockwise and anti−clockwise will give a measure of symmetry. Large values will be associated with asymmetry, small with symmetry in the curvature description. A modification of this method in which every outline point over half the outline is used as a start point and the minimum overall difference calculated would reduce subjectivity in the definition of an axis of symmetry.

Bookstein (1977) has suggested that it is possible to compare forms by sampling the tangent angle function (arc length and tangent angle) at landmarks and submitting these values to multivariate statistical analysis. Where the use of landmarks is not desirable or possible some criterion such as least squares might be applied to the determination of "equivalent" start points and tangent angles at regularly spaced intervals compared.

## Polar co-ordinates

Earlier it was noted that Cartesian co-ordinate pairs are inappropriate for direct shape comparison. The shapes to be compared must either be registered in a way that imparts some comparability in co-ordinates, or registration invariant measures of shape need to be calculated.

One method of circumventing these problems is to re-express the Cartesian pairs as polar pairs centred on the objects themselves. This is achieved by determining on each shape an origin for the polar series and a point on the outline from which the series will be deemed to begin. The line connecting origin to start point is the line to which all other polar co-ordinates are referred. If the origin and start point are "homologous landmarks" (e.g. Lestrel, 1982) then all comparisons between polar co-ordinate pairs from outlines are in effect referred to these homologies. The biological validity of such a procedure is debatable because polar co-ordinates with the same angular displacement (other than the reference co-ordinates) taken from different individuals may pass through what may be considered non-homologous points on the outlines. Conversely, homologous points, other than those used for reference, may lie at different angular displacements from the zero axis. The biological sense in comparing successive polar co-ordinates from different shapes seems limited. Any errors in the identification of the reference points will affect all the polar series, errors in the location of the origin are "expressed in the alteration of every value of the radial function....in a complex and non-linear way" (Bookstein, 1977).

Polar co-ordinates may also be used in the comparison of shapes without any attempt to define homologies. In this case the origin for the series can be a

mathematically determined point such as the centre of area, and the start point can be likewise specified without any biological reference, e.g. randomly after "least squares fitting". Size is equalised by scaling to equal areas. This is an attempt to describe shape *per se*: the positions of homologies are not under study. The function will, almost certainly, embody some biological non-equivalences between shapes (e.g. homologies mismatched in terms of angle or radius). This does not matter for we are interested in "mathematical" shape differences, which, like differences in the disposition of homologies, may concern biologists.

Polar co-ordinates in themselves have been infrequently applied to the study of biological forms. The reasons for this are primarily that any regional differences demonstrated between the forms suffer the handicaps of being registration dependent and that only shapes without re-entrants are amenable to analysis by this technique.

Yasui (1986) has used polar co-ordinates to study shape variation in Japanese crania. He orientates outlines with respect to each other not by a fixed outline point, but by rotating them and determining a criterion of best fit. This is similar to the approach of O'Higgins, Johnson and McAndrew (1986). Yasui corrected for size differences between crania by determining the allometric relationship between each polar radius and the area enclosed by the outline.

Great care is needed in the interpretation of apparent regional differences in outlines as demonstrated by the polar method. They are entirely registration dependent. The only thing that can be determined with any certainty is that outlines are different, and then only after they have been equalised for size, rotation and translation. The way in which translation and rotation are standardised will critically modify the degree of observed difference. There is a good argument

in favour of a registration which minimises the misfit of outlines (as measured by residual area between them). The minimum residual area, after size differences are eliminated, can be taken to reflect shape difference (identical "shapes" would have zero mismatch).

## Fourier analysis

The single Fourier series has been applied to shape measurement in many disciplines: it is a standard technique and descriptions of it can be found in standard texts. It is particularly suitable for the measurement of smoothly varying forms because it attempts to decompose these into a series of sinusoidal waves of differing frequencies, phases and amplitudes which when summated give a good approximation to the original. It has been applied to the measurement of biological shapes by a number of workers (e.g. Lu, 1965, Kaesler and Waters, 1972, Lestrel, 1982, Ferson, Rohlf and Archie, 1984, Rohlf, and Koehn, 1985).

Briefly, a circular function, $f(\theta)$, e.g. polar co-ordinates, tangent angle, or curvature can be approximated by;

$$f(\theta) = a_0 + \sum_{i=1}^{N} a_i \cos i\theta + \sum_{i=1}^{N} b_i \sin i\theta$$

the $a_i$'s are the cosine components, and the $b_i$'s are the sine components, they describe the amplitude of cosine and sine waves at a particular frequency, given by i. N is the maximum harmonic order of the calculated series. The effect of summation of sine and cosine waves of differing frequency and amplitude is illustrated in fig. 2.7. The single Fourier series will provide a fit to any smooth single-valued function. It is possible to calculate Fourier series directly from x and y co-ordinates (Zahn and Roskies, 1972). Rohlf and Archie (1984) have used such techniques to directly determine an elliptic Fourier series. Converting data from one form to another (e.g. curvatures to Fourier coefficients) might seem

FIGURE 2.7 – The effect of serial addition of waves of differing frequency and amplitude. The square wave in the top frame is approximated successively in the lower frames

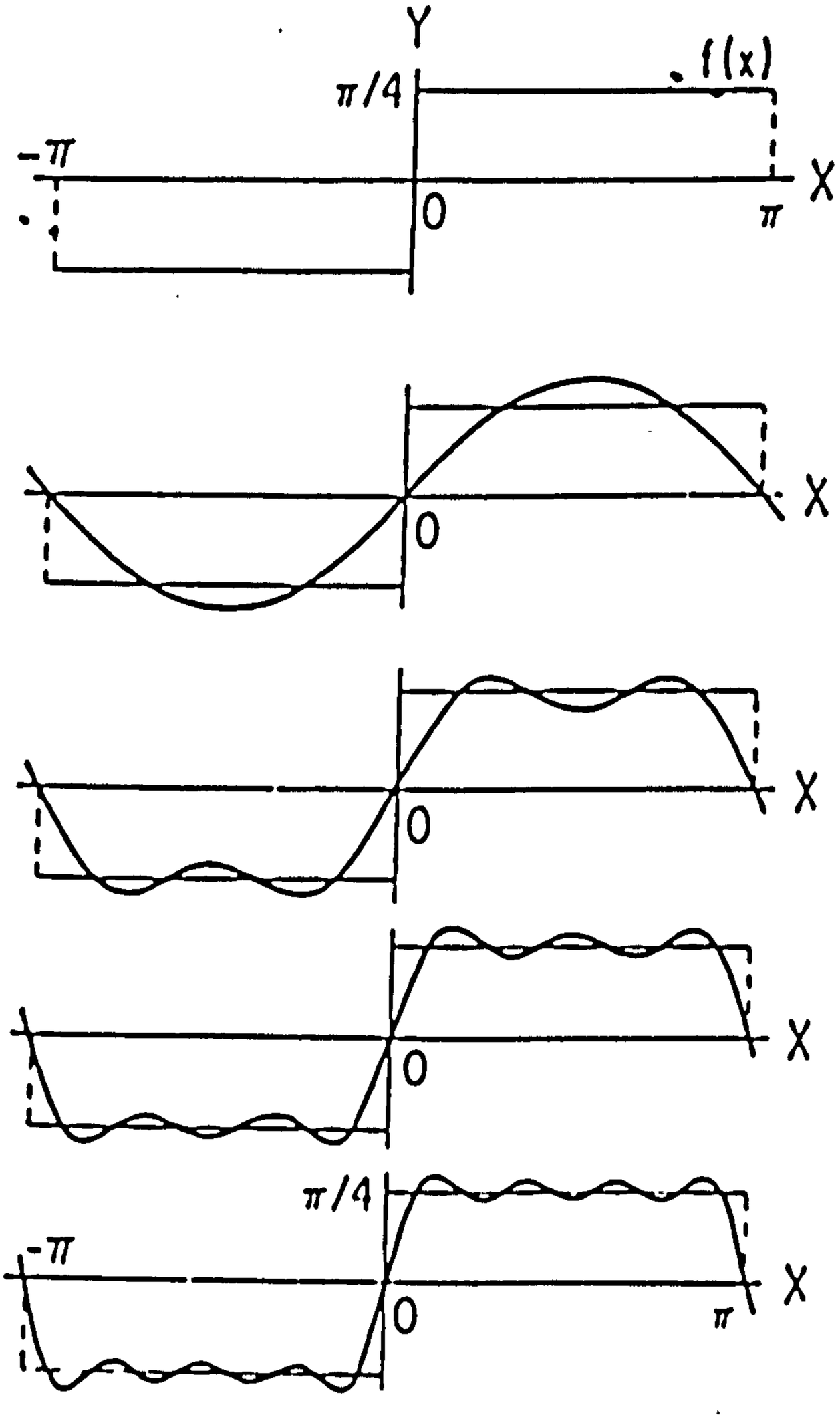



Fig 2.7

illogical but the Fourier series has several properties which are potentially useful.

In the sine–cosine form shown above, the value of each component is dependent on the "start point" for the series, the sine and cosine components are orthogonal to each other. If applied to bilaterally symmetrical objects (e.g. vertebrae, O'Higgins, Johnson, and McAndrew, 1986) when the start point coincides with an outline point on the axis of symmetry, the sine terms will be equal to zero (in practice they will tend to zero because of measurement error). Rotate the start point through 90° and the cosine terms will be zero. The Fourier series can thus be useful in the study of symmetry. The Fourier series, being made up of sine and cosine terms represents the transformation of data from a spatial to a frequency domain. As many biological objects have relatively slowly undulating outlines, the shape may be adequately described by relatively few Fourier components. Furthermore the frequency characteristics of outlines can be compared by examination of their "power spectra" which represent the relative total amplitudes of the various harmonics.

The Fourier series converges onto the measured form as more components are calculated. It therefore allows reconstruction of the measured form. Figure 2.8 illustrates a chimpanzee cranium which is reconstructed from increasing numbers of Fourier components via polar co–ordinates.

There is an alternative representation of the Fourier series, the amplitude–phase–lag representation;

$$f(\theta) = R_o + \sum_{i=1}^{N} R_i \cos(i(\theta + \Phi_i)$$

FIGURE 2.8 – The reproduction of an outline taken from a chimpanzee cranium by adding successive Fourier coefficients. Figures in the top right of each frame indicate the number of Fourier coefficients used.

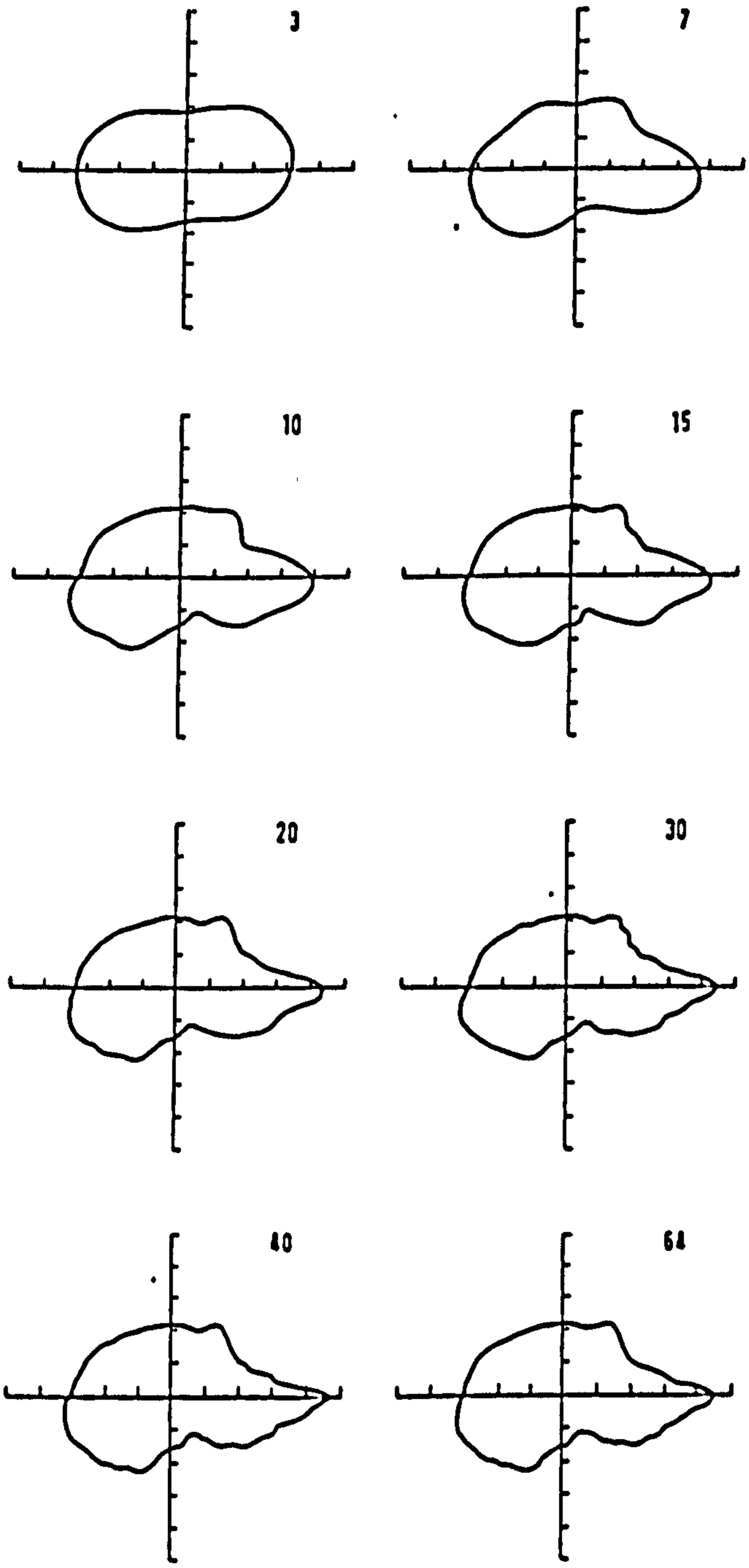



Fig 2.8

The R's are known as the amplitude components and the Φ's as the phase lag components. The phase lag components contain all the information about "start point", i.e. they "register" the waves of different frequency "on top" of each other in a way that allows reconstruction of the original outline. This can be turned to advantage. In situations where dependency on start point definition is considered a disadvantage the amplitude components alone can be compared between shapes. O'Higgins and Williams (1987) have shown, in a study of cranial form in primates, that analysis of the amplitude spectrum gives a similar pattern of between species discrimination to that resulting from analysis of the combined amplitude/phase-lag spectrum. The degree of between OTU discrimination in the former analysis was, however, reduced relative to that in the latter.

Fourier analysis as a means of describing biological forms and form differences has been criticised by Bookstein (1978) and Bookstein *et al.*, (1982) on several grounds. He states that Fourier decomposition of a curvature function around an outline allows for one landmark only, the startpoint. If the aim of study is to examine differences in homology relationships then homologies will be undiscernible from the Fourier coefficients. Bookstein (1978) has also criticised the Fourier decomposition of chain coded data because the curvature function from such outline representations is not smooth, but rather it represents sudden jumps of integral. The series converges with increasing coefficients not to a smooth curve but to a jerky outline. Both of these criticisms are true. The description of the pattern of disposition of homologies is confused, not aided by Fourier analysis. We have seen however that the biologist may on occasion wish to measure form, not as a map of biological homologies but as shape in a purely mathematical sense, in this case there can be no assumption of homologies between forms

(other than the forms themselves – e.g. whole crania). In this limited application Fourier analysis is as valid as any other approach to "pure" shape analysis. The fact that chain coded data give rise to jerky outline representations is of interest, but not a death blow. There are techniques for data smoothing which have been applied in image processing and which can be applied to biological studies (see Gonzalez and Wintz, 1977).

Bookstein (1978) continues his criticism of Fourier analysis by considering the Fourier decomposition of polar data. Just as polar co-ordinates are prone to widespread change with differences in the location of the origin so are Fourier coefficients, but in a highly complex way. If the origin is taken as an homology, this is serious, if the origin is determined by some aspect of shape and the objective is to study "mathematical" shape, then the same comments as above apply.

Erlich, Baxter-Pharr, and Healy-Williams (1983) have replied to these criticisms. They point out that "examination of homologous skeletal features is only one of many approaches" to biomorphological studies. They examine the relationship between specific homologies and individual components of the Fourier series. They demonstrate from data collected on the foraminiferan *Globorotalia trucatulinoides* that there is a "consistent angular relationship between the orientation of the second harmonic and the spiral side keel". With this noted they indicate that it might be suggested that "the very fact that the radial Fourier series is locking on to homologous points is a good reason not to use the Fourier series; that is, given the relationship why go through the complex calculations?".

The justification they give is that "the possibility always exists, however, that the additional data needed to fully reconstruct the profile between homologous points may contain biologically interesting information". This is true but, given the complex relation between form and Fourier components, it is not necessarily the optimal way of describing shape between landmarks, Bookstein (1977) has previously suggested conic splining for this purpose. Further justification for the use of Fourier analysis is given by the fact that since it is a convergent series, it may allow the reduction in data quantity per form (see above).

A more extensive reply to the comments of Bookstein *et al.* (1982) has been furnished by Read and Lestrel (1986). These workers provide an example in which measurements taken between homologous points fail to describe significant differences in morphology between structures because the measurements omit the boundary connecting the landmarks.

Read and Lestrel (1986) express agreement with the observation made by Bookstein *et al.* (1985:3) that "although no morphometric method can be wrong in all contexts, neither is any method universally applicable". As a step towards a more generally applicable morphometric methodology Read and Lestrel propose a system of shape representation in which both boundary and homologous point information is encoded by a combination of Fourier analysis and a local co-ordinate system.

Read and Lestrel (1986) conclude that "the Fourier system of representation has been very effective for ...descriptive work" especially where "the emphasis has been more on descriptive techniques that are sensitive to biologically significant differences in the form of shapes than on the representation of the growth

process".

Shape description – concluding remarks

The study of shape as an object in its own right follows well worked out methods developed in a variety of other fields. It allows no biological statements about changes in regions from one shape to another, which would involve a determination of homologies. It does allow the construction of several "shape equivalence" classes, for instance shapes with the same perimeters and areas, the same "bending energy", etc. These in themselves are not, in general, biologically meaningful entities, but they do conform to ideas about perceived shape similarities. They may be useful in sorting out what is meant by "evolutionary convergence" when the term is applied to form.

These shape measures are also of use when homologies are undefinable, for instance the "homology problem" described above (Sneath and Sokal, 1973) or in studies of certain creatures for instance amoebae (pseudopodia cannot really be considered homologous in the same way as limbs can between mammals).

Traditional biometrics has until recently been concerned only with "homology map" differences in the study of biological "forms". Recent studies have been directed to the study of "mathematical" or "boundary shape" differences. The comparison of results obtained by both approaches might prove a fruitful area of investigation.

There is a need for the development of a probablistic model of homology of form.

# A STUDY TO EMPIRICALLY EXAMINE THE RELATIVE PERFORMANCE OF A NUMBER OF NEW BIOMETRIC TECHNIQUES IN THE STUDY OF CRANIAL FORM

## INTRODUCTION

In the earlier parts of this chapter I have discussed a number of problems associated with traditional approaches to craniometry and have reviewed some promising new approaches to biometry. I now describe a study which compares the results obtained using the new methods with those obtained using the old.

There are good theoretical reasons why each of the methods used in this study should be able to provide a measure of form. The relative merits of the methods are, however, unknown. Earlier in this chapter I have examined the important philosophical differences between descriptions of biological structures based upon landmarks and those which are landmark independent and have pointed out that comparisons using the first type of description examine shifts in homologies relative to each other and the second, shape differences. This must be borne in mind when questions about relative efficacy are being asked – effective for what? Only when shape differences are highly correlated with homology map differences (as they are likely to be when the majority of postulated homologies are features of shape) are the two groups of methods likely to be interchangeable. In every other situation disparities observed using each of the methods relate to shape change independent of homology shift or visa versa. I have already noted that this may turn out to be a useful approach to the study of shape convergence, possibly

providing a partial answer to the question of skulls of similar shape being brought into being by dissimilar morphogenetic processes.

In this chapter, I describe the pattern of homologies of the crania of chimpanzees, gorillas, orang utangs, and man by means of a number of linear and angular dimensions taken between a series of landmarks. The patterns of variation within and between these groups are examined by a series of statistical analyses and graphical procedures. The effect of converting these data to indices is determined empirically. The patterns of variation which are revealed by least square fitting of the co-ordinates of landmarks in the median plane (after Sneath, 1967) are also compared.

Two methods that offer a degree of independence of the homology map are then applied to the midline tracings of the same collection of specimens. These are the methods of Fourier analysis, and "shape factors". The resultant patterns of variation are then compared with each other and with those produced from the previous three investigations. Some general conclusions can be drawn relating to the problems encountered in the study of biological form.

# MATERIALS AND METHODS

## A. Materials

Mensural data were collected from 175 skulls of extant apes (54 *Pongo*, 60 *Pan*, 61 *Gorilla*) and from 124 skulls from each of the principal racial groups of the extant Hominidae. Their provenance is detailed in Table 2.1.

Attention was restricted to adult specimens in which, in apes, the full permanent dentition (including the canines and third molars) had erupted and was aligned and, in the case of man, in which the full permanent dentition (less possibly one or more of the third molar teeth) was aligned and the sphenoccipital synchondrosis was fully fused.

In both human and ape material only those skulls were included which were sufficiently complete to permit full sets of measurements to be taken.

### Sexing

The sexes of the skulls of *Pan* and *Gorilla* were known from field records and were checked against the skins which are also available in the collections. Those of *Pongo*, which were not known from documentation, were sexed visually on the basis of the established dimorphism in size, and in the degree of development of muscular markings, crests and canine teeth.

The sexes of the caucasoid group of human skulls were obtained from parish records. The sexes of the three remaining groups of human skulls (negroid, mongoloid, australoid) were not documented and, in view of the established

uncertainty in sexing human skulls, no attempt was made to divide into male and female subgroups on the basis of anatomical criteria.

## TABLE 2.1

### The Number and Provenance of Skulls of Extant Hominoidea

| Group | No of skulls | Provenance |
|---|---|---|
| *Pongo* sp. | 54 | British Museum (Natural History), Department of Zoology.<br>Royal College of Surgeons, London, Odontological Museum.<br>University College London, Department of Anatomy.<br>University of Leeds, Department of Anatomy.<br>University of Birmingham, Department of Anatomy.<br>Duckworth laboratory of Physical Anthropology, University of Cambridge.<br>Royal Scottish Museum, Edinburgh |
| *Pan* sp. | 60 | Powell Cotton Museum, Birchington |
| *Gorilla* sp. | 61 | Powell Cotton Museum, Birchington. |
| *Homo sapiens* (caucasoid) | 30 | St. Bride's Church, London |
| *Homo sapiens* (negroid) | 30 | British Museum (Natural History) Department of Paleontology. |
| *Homo sapiens* (mongoloid) | 30 | British Museum (Natural History), Department of Paleontology. |
| *Homo sapiens* (australoid) | 30 | British Museum (Natural History), Department of Paleontology. The Royal College of Surgeons, London, Odontological Museum. |

## B. Methods

### I. Definition of size

Size and shape are intimately linked in a mathematical way, such that in the absence of equality in shape no unambiguous definition of size can be made.

Some of the methods of form description used in this study result in dimensionless variables whilst others do not. The patterns of phenetic relationships demonstrated between groups using dimensionless descriptions will not, by definition, reflect simple (non-allometric) size differences. Those patterns derived from linear and angular measurements will be influenced by size as well as shape differences. The problem of reducing the influence of size on these patterns arises if they are to be compared with those derived from dimensionless variables.

In the case of two objects, A and B, with identical ratios of dimensions (equal shape) the difference in scale or size between them is given by the ratio of any variable $a_n$ with its counterpart $b_n$.

Comparisons are often made between objects which differ in shape. The biologist has an intuitive notion of relative size between these objects. The strict description of this size difference is, however, elusive. The fact that the objects are of different shape means that comparisons between any pair of dimensions, one from each object, will no longer reflect size differences alone, their total difference will be the result of size and shape difference. The problem is one of determining a measure which constitutes a good reflection of the biologist's intuitively determined size difference. This problem is considered by Sneath and Sokal (1973,

p169–170). They state that size may be thought of as a general factor that affects many characters; it is a function of the magnitude of the states of many characters. Shape, they consider, must necessarily refer to ratios between different characters.

Most studies which examine the phenetic relationships between organisms make some reference to size differences. From the above considerations, however, it is clear that size is a vague concept when applied to organisms of different shape. As objects become more different in shape, then the definition of size differences becomes more ambiguous. Sneath and Sokal see the dilemma as exemplified by the question "which is bigger, a snake or a turtle?". The problem applies to a lesser extent to this study. The crania of the men and those of the apes are different in shape. It is therefore impossible to produce a single, unequivocal, mathematical definition of cranial size.

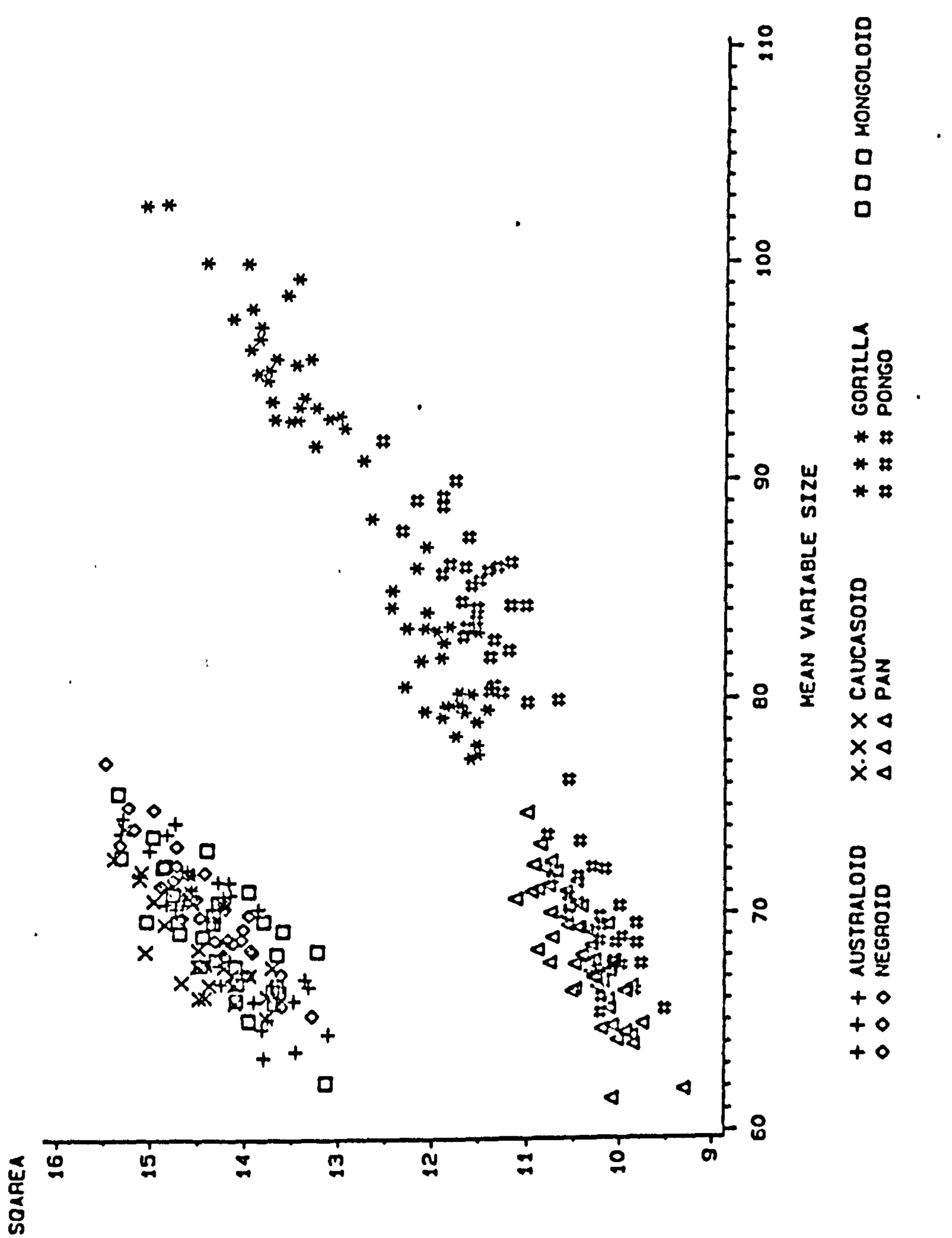
A number of workers have employed several different measures to express overall size difference in studies of cranial form. Wood (1976) used femur length as an estimate of body size and determined the allometric relationship between this and a number of cranial and other dimensions. He also attempted to partition the differences between taxa into size and shape components using Penrose's (1954) size and shape differences. The Penrose size difference is essentially the square of the difference between character sizes in two organisms.

Creel and Preuschoft (1984) used the Sneath size variable (see later) as a measure of cranial volume. This was used to adjust cranial measurements allometrically. This differs from both of Wood's measures of size. Albrecht (1978b) used three different measures of size in a study of the craniofacial morphology of the Sulawesi macaques: the greatest length of each skull, the geometric mean of the log transformed variables and an estimate of cranial volume. He showed

that these variables have a correlation greater than 0.96 with each other in these taxa. This reflects the generally similar morphology of the crania.

The choice of a size variable is largely a matter of intuition. In this study the use of two different size variables was considered, the mean value of all linear dimensions and the square root of the area of the midline tracing of each cranium. No data on body weight, or from the post cranium were available. Figure 2.9 shows a plot of the scores of each cranium on each size variable. This graph emphasises the fact that different size measures may well reflect different things about crania of different shapes. Within the apes and within the men the two variables show a near straight line relationship. The mean within group correlation between the two variables was 0.86. The two size measures differ: in terms of the square root of the midline area the men are relatively large: in terms of the mean variable size they are relatively small. This reflects the relatively large size of the neurocranium in men and the fact that more linear and angular dimensions could be taken from the face and cranial base.

FIGURE 29 – Bivariate plot of the scores of crania on each of two size variables. Vertical axis = square root of midline area, horizontal axis = mean of all linear dimensions.



An attempt to eliminate size effects in the observed pattern of between group relationships using one of these variables will likely give different results from those using the other. The choice is arbitrary, yet the effect is intuitively real, size differences will impinge on our perception of overall differences. Certainly the differences between the groups of apes and those of men will be accentuated by size differences and both size measures will serve well to reduce this effect if used to scale the data. The size measures will, however, have different effects on the perceived ape–human distances. Fortunately, it seems, this problem is more theoretical than practical. Comparison of distance matrices computed using linear dimensions adjusted against square root of midline area and against mean dimension showed a correlation of $>0.9$ ($P<0.01$). The influence upon observed ape–human distances was minimal.

It seems that in this study the major difference between groups is one of shape and not size. It was decided to use the square root of the sagittal area as the size measure in all subsequent analyses on the grounds that it takes even account of all anatomical regions of the cranium, is more independent of individual linear dimensions, is suitable for size adjustment of Fourier coefficients (having a clear mathematical relationship to them – see later) and that it is closely related to the Sneath size measure which is used in this study to construct a distance matrix based upon the methodology described in Sneath's (1967) paper.

## II. Definition of shape

Several methods were applied to the description of cranial shape. These were not derived to emphasise particular differences in cranial morphology, say between men and apes, but rather to sample cranial morphology as evenly as possible. Any overconcentration of measurements in particular anatomical regions is a consequence of the methods themselves. For instance the cranial vault, especially in humans, accounts for a major part of the whole cranium, but presents few identifiable landmarks per unit area relative to the face or base. The linear and angular mesurements therefore tend to be concentrated in these regions.

The collection of the linear and angular dimensions and the production of tracings of the mid-sagittal plane of the whole of this material was undertaken by the late Professor E.H. Ashton and by Professor W.J. Moore.

a) Cranial angles and linear dimensions

A common approach to the description of cranial morphology entails the use of linear and angular measurements taken between defined (homologous) osteometric landmarks (e.g. Boule, 1911a, 1911b, Morant, 1926, 1927, 1928, 1930, 1936, Howells, 1973). Angular measurements are dimensionless and are, effectively, indices. More recent studies tend to use linear measurements and exclude angles (e.g. Bilsborough, 1972, 1973, Stringer, 1974a, Brauer, 1984, Bilsborough and Wood, 1988) because of the difficulties in obtaining such measures and because of those associated with the statistical properties of ratios (see earlier and Atchley *et al.*, 1976). In this study it was decided to mix both angles and indices, following older established practice (in any case the results of preliminary analyses including and excluding angular quantities from the data showed little if any difference in the consequent phenetic relations of extant groups).

Twenty five landmarks, (Table 2.2), defined by Trevor, (1950) covering the cranial vault, facial skeleton and mandible were located on each cranium and a series of linear and angular measurements taken between them. It seems likely that there is a general correspondence in most of the landmarks between the several hominoid groups in the study, apart from the nasion. In *Homo sapiens*, where the nasofrontal suture normally lies horizontally, the nasion is situated at the root of the nose. In apes, where the suture forms an inverted "V", it may be located some distance into the frontal region. As a result the line joining the anterior border of the pituitary fossa to the nasion lies along the floor of the anterior cranial fossa in man but not in apes. If the nasion in apes is redefined as the point at which the line joining the most superior points on the frontal processes of the maxillae cuts the internasal suture a better anatomical equivalence

## TABLE 22

## LANDMARKS

| Name | Abbr. | Definition | Use in apcs |
|---|---|---|---|
| **1. Cranium** | | | |
| apex | apx | highest point on vault in transverse plane | Adjust for sagittal crest if necessary as for bregma |
| basion | ba | lowest point on anterior external surface of foramen magnum in median plane | – |
| bregma | b | point at which sutures meet between frontal and two parietals | Adjust for sagittal crest if necessary by following contour of vault below sagittal crest |
| endomolare | enm | mid point, inner margin of socket of upper second molar | |
| glabella | g | most prominent point between supraciliary arches in median plane | – |
| infradentale | id | mid point of line tangential to outer margins of sockets of upper incisors | – |
| infraorbitale | ib | highest point on rim of infraorbital foramen | major foramen when multiple |
| lambda | l | point at which sutures between occipital and two parietal bones meet | Adjust for sagittal and nuchal crests if necessary – as for bregma |
| maxillo–frontale | mf | point at which anterior lacrimal crest, continued, meets suture between maxillary and frontal bones | – |
| nariale | na | point where line joining lowest points on inferior margin of nasal aperture on each side crosses the median plane | margin of nasal aperture continued to anterior nasal spine |
| nasion | n | mid point of suture between frontal and two nasal bones | point where line joining uppermost points on maxillae crosses median plane |
| opisthion | o | point at which external and internal surfaces of occipital bone meet on posterior margin of foramen magnum in median plane | – |

| Name | Abbr. | Definition | Use in apes |
|---|---|---|---|
| opisthocranion | op | most posterior point on cranial vault in median plane | Adjust for sagittal and nuchal crests if necessary – as for bregma |
| orbitale | or | lowest point on inferior margin of orbit | – |
| porion | po | highest point on margin of external acoustic meatus | – |
| prosthion | pr | most prominent point on alveolar process between sockets of upper incisors | – |
| staphylion | sta | point at which line tangential to the two curves on posterior border of palate crosses interpalatine suture | – |
| subsymphyseale | ssy | lowest point on mandibular symphysis | – |
| **2 Mandible** | | | |
| condylon | co | highest point on mandibular condyle | – |
| coronion | cr | highest point on coronoid process | – |
| ectomolare | ecm | mid point outer alveolar margin of lower second molar | – |
| ectopremolare | ecp | mid point outer alveolar margin of lower first premolar | – |
| gonion | go | point on angle nearest zero axis | – |
| mandibular foramen | mbf | lower point on margin of foramen | – |
| mental foramen | mtf | lowest point on margin of foramen | major foramen where multiple |

is attained (subject to the considerations discussed earlier in this chapter, some of which were conceived after the data had been collected).

In adult apes especially the male specimens of *Pongo* and *Gorilla*, the opisthocranion which is intended to represent the most dorsal point on the braincase is further displaced by the development of prominent muscular cresting. If again the apex is intended to be the highest point on the vault in the mid-sagittal plane the prominence of sagittal cresting in these groups leads to a disparity in the definition. For these reasons the craniometric landmarks were estimated as if nuchal and sagittal cresting were not developed.

*Method of measurement*

A series of 47 linear dimensions and 12 angles was taken between the defined craniometric points (table 2.3). Many of these have been described in standard texts (Buxton and Morant, 1933; Howells, 1936; Morant, 1936; Trevor, 1950), though in certain cases their definitions have been modified for the reasons outlined above. Linear measurements in horizontal and coronal planes were taken with sliding or spreading callipers. The mandibular angle was taken with a mandibular board.

Linear and angular measurements in the midline were taken with a steel ruler or protractor on sagittal tracings taken with the craniostat described by Ashton and Pardoe (1950). The modified projector specially developed for use in studies of the innominate bone (Zuckerman, Ashton, Flinn, Oxnard and Spence, 1973) was used for this purpose. The sagittal outline was projected at intervals of 1mm., excluding the nuchal and sagittal crests (if present), the positions of

## TABLE 23

## MEASUREMENTS

| Name | Definition |
|---|---|
| **Neurocranium** | |
| Maximum length | g – op |
| Maximum breadth | Between parietal bones, perpendicular to median plane (in apes taken immediately above mastoid crests) |
| Basibregmatic height | ba – b |
| Auricular height | po – apx |
| Postorbital breadth | Maximum transverse breadth immediately posterior to orbital processes of zygomatic bones |
| Frontal height | Perpendicular distance from frontal chord to most remote point on frontal arc |
| Frontal chord | n – b |
| Parietal height | Perpendicular distance from parietal chord to most remote point on parietal arc |
| Parietal chord | b – l |
| Occipital height | Perpendicular distance from occipital chord to most remote point on occipital arc |
| Occipital chord | l – o |
| Foramen magnum length | o – ba |
| Foramen magnum breadth | Maximum internal breadth perpendicular to length |
| Angles | b – l – o<br>l – o – ba |
| **Viscerocranium** | |
| Total facial height | n – ssy |
| Upper facial height | n – pr |
| Palatal length | sta – pr |
| Palatal breadth | enm – enm |

| Name | Definition |
|---|---|
| Nasal breadth | Maximum breadth of nasal aperture between anterior surfaces of lateral margins |
| Nasal height | n – na |
| Subnasal height | na – pr |
| Orbital height | Maximum internal height of orbit perpendicular to breadth |
| Orbital breadth | Maximum breadth from mf to anterior rim of lateral orbital margin |
| Infraorbital breadth | ib – ib |
| Bizygomatic breadth | Maximum breadth between zygomatic arches |
| Maxillo – mandibular height | ib – mtf |
| Mandible | |
| Projective length mandible | Zero axis of standard horizontal (shp) and transverse (stp) planes to most projecting point on chin (in apes to most anterior point on body of mandible) |
| Projective length corpus | Zero axis of standard horizontal and standard rameal planes to most projecting point on chin |
| Projective height ramus | From standard horizontal plane to ecm perpendicular to shp |
| Projective height | Zero axis standard horizontal plane and standard rameal plane to co |
| Minimum rameal breadth | Minimum distance between anterior and posterior borders |
| Projective height coronoid | Zero axis (shp/stp) – cr |
| Coronial breadth | cr – cr |
| Condylar length | Maximum distance from medial to lateral condylar pole |
| Bicondylar breadth | Maximum breadth between lateral poles of condyles |
| Bimental breadth | mtf – mtf |
| Bigonial breadth | go – go |
| Symphyseal height | id – ssy |
| Mandibular angle | Between standard horizontal and rameal planes |
| Molar – premolar chord | ecm – ecp |

| Name | Definition |
|---|---|
| Angle | go – ssy – id |
| **C. Viscerocranial – Neurocranial Relationships** | |
| Upper viscerocranium | |
| Basi-infraorbital length | ba – ib |
| Basi-nasal length | ba – n |
| Basi-prosthion length | ba – pr |
| Basistaphylion length | ba – sta |
| Lower Viscerocranium | |
| Basigonion length | ba – go |
| Basi-infradentale length | ba – id |
| Basimandibular length | ba – mbf |
| Basimental length | ba – mtf |
| Basisymphyseal length | ba – ssy |
| Angles | ba – n – b<br>ba – n – pr<br>n – b – l<br>b – ba – pr<br>o – ba – n |
| | ba – go – ssy<br>ba – n – ssy<br>n – ba – ssy |

the midline craniometric points were carefully marked on the tracing.

*Precision of measurement*

Angular measurements were recorded to the nearest degree and linear dimensions to the nearest 1mm.

Five sets of repeat measurements were taken from five female chimpanzee crania which were selected to be as similar as possible. Similar repeat sets of measurements were taken from a series of five human skulls (caucasoids) which were selected at random. An analysis of variance showed that artificially introduced inconsistencies of measurement were insignificant ($P>0.01$) in all of the 59 measurements taken from the human sample, but in the case of the chimpanzees two measurements seemed to be unreliable. Further examination of the data showed that the chimpanzee skulls did not vary in these dimensions. It is unlikely that errors in measurement could have had a significant effect on the overall results.

*Effects of size*

The linear dimensions vary between crania because of both size and shape differences. In the first set of studies to be described in this chapter raw (non-size adjusted) data were used. However, some of the methods of cranial measurement result in size independent data and in order to allow comparison between each method of cranial description (the second part of this study) the linear dimensions were scaled by ratio with respect to the square root of the area of the mid-sagittal projection (variable x constant /size variable, where the constant was chosen such that the transformed variables have a magnitude similar

to the original variable). The result of such a manipulation is that each transformed variable is effectively a ratio quantity and as such might be expected to suffer from the problems associated with indices (see earlier and Atchley *et al.*, 1976). The degree of alteration of the phenetic relationships of OTUs that can be attributed to the use of (scaling) indices can be assessed by comparison of the results of analyses using raw and adjusted data (see later).

b) Cranial indices

A frequently used method of expressing shape is to construct indices which serve to describe either a structural or functional unit in a way which is concise and which allows simple statistical comparison. Indices are summary measures insofar as they represent the compound of two dimensions, and, subject to the observations of Atchley *et al.* (1976) and Albrecht (1978a), they are size independent (allometric considerations aside).

Indices are infrequently used in multivariate craniometry in the West, though Howells (1973:184) has indicated that they are in more common usage in the Russian literature. Furthermore, indices were certainly in common usage in early biometric studies (e.g. the studies of Broca, 1911a, Morant, 1927, 1928, 1930, 1936). The data which were available for this study allowed a set of indices and angles (which are themselves indices of sorts) to be submitted to multivariate study. The resulting phenetic relationships implied by this data, in turn, allow an empirical study of the consequences of using indices.

For the purposes of this study a series of 53 indices were constructed to describe aspects of neurocranial, viscerocranial and mandibular shape and to express aspects of their relative proportions and interrelationships (table 2.4). These indices whilst being dimensionless quantities were not constructed with the express purpose of scaling the data (c.f. previous section).

*Method of calculation*

The indices were calculated from the series of measurements described above, and were combined with the twelve angular measurements. The data comprised a total of 65 variates from each skull.

# TABLE 24

## INDICES

1. NEUROCRANIUM

Maximum breadth/maximum length

Postorbital breadth/maximum length

Basibregmatic height/maximum length

Auricular height/maximum length

Basibregmatic height/maximum breadth

Auricular height/maximum breadth

Frontal chord/frontal height

Parietal chord/parietal height

Occipital chord/occipital height

Foraminal breadth/foraminal length

2. VISCEROCRANIUM

Nasal height/subnasal height

Nasal breadth/nasal height

Upper facial height/infraorbital breadth

Upper facial height/palatal length

Orbital height/orbital breadth

Palatal breadth/palatal length

Bizygomatic breadth/palatal length

Infraorbital breadth/palatal length

3. MANDIBLE

Projected height ramus/bicondylar breadth

Projected height corpus/bicondylar breadth

Projected height ramus/projected length mandible

Projected height corpus/projected length mandible

Bicondylar breadth/projected length mandible

Coronial breadth/projected length mandible

Bigonial breadth/projected length mandible

Bimental breadth/projected length mandible

Projected height ramus/projected height coronoid

Projected height corpus/projected height ramus

Minimum rameal breadth/projected length corpus

Projected height ramus/minimum rameal breadth

Projected height corpus/projected length corpus

Coronial breadth/bicondylar breadth

Bigonial breadth/bicondylar breadth

Molar – premolar chord/projected length corpus

Condylar length/bigonial length

Bimental breadth/bigonial breadth

4. NEUROCRANIAL – VISCEROCRANIAL RELATIONSHIPS

Basi – infraorbital length/basinasal length

Basimental length/basinasal length

Basi – infradentale length/basinasal length

Basi – infraorbital length/basimental length

Basi – prosthion length/basi – infradentale length

Basi – prosthion length/basi – nasal length

Basisymphyseal length/basinasal length

Basisymphyseal length/basigonial length

Basigonial length/basinasal length

Basimandibular length/basinasal length

Maximum length braincase/palatal length

Maximum length braincase/projected length mandible

Maximum length braincase/infraorbital breadth

Maximum breadth braincase/bicondylar breadth

Basibregmatic height/total facial height

5. NEUROCRANIAL – MANDIBULAR RELATIONSHIPS

Upper facial height/symphyseal height

Maxillo – mandibular height/total facial height

*Precision of measurement*

An analysis of variance was performed in a similar manner as for the linear dimensions and angles. In the human sample inconsistencies introduced by errors of measurement were insignificant in all cases ($P<0.01$). Three indices were virtually invariant between the chimpanzee crania and in these cases the errors of measurement were statistically significant, this result did not invalidate their use in subsequent analyses.

*Effects of size*

Each index and angular quantity is a dimensionless measure of an aspect of shape.

c) Method of least squares

Sneath (1967), described a method for comparing two forms on the basis of a series of "corresponding" landmarks. He calculated a measure of fit, Dh, the root mean square distance between pairs of landmarks (one taken from each structure) and showed how this could be applied to the study of cranial form.

In the comparison of two-dimensional forms such as sagittal cranial tracings, the X,Y co-ordinates of the landmarks are recorded, and used to calculate a centroid, Xmean, and Ymean for each shape. In order to standardise the "overall size" of each object the original X,Y co-ordinates of the landmarks are expressed in terms of the standard deviation of their distances from the centroid. The transformed co-ordinates, x',y' are given by:

$$x' = (X - Xmean)/S_{x,y}$$

$$y' = (Y - Ymean)/S_{x,y}$$

where,

$S_{x,y}$ is the standard deviation of the distances of the landmarks from the centroid

x' and y' are the transformed co-ordinates

and X and Y are the original co-ordinates.

The measure of fit, Dh, between the pairs of landmarks is calculated as follows:

$$D_h^2 = Dmin^2/h$$

where,

h= the number of landmarks

and

$Dmin^2$ = the minimum value obtained from,

$$\sum_{i=1}^{h} ((x'_{Ai} - x'_{Bi})^2 + (y'_{Ai} - y'_{Bi})^2)$$

when the shapes are rotated or reflected relative to each other about the centroid, and Ai and Bi are a pair of corresponding landmarks.

The fit coefficient, $D_h$ allows the comparison of two shapes with respect to each other, the more similar the shapes, the smaller the coefficient.

*Method of measurement*

11 craniometric points were defined on the mid-sagittal tracings of the cranial series. The placement of these points is shown in fig. 2.10 and their

FIGURE 2.10 – The placement of the landmarks used for the calculation of Sneath's $D_h$. Abbreviations are listed in Table 2.2

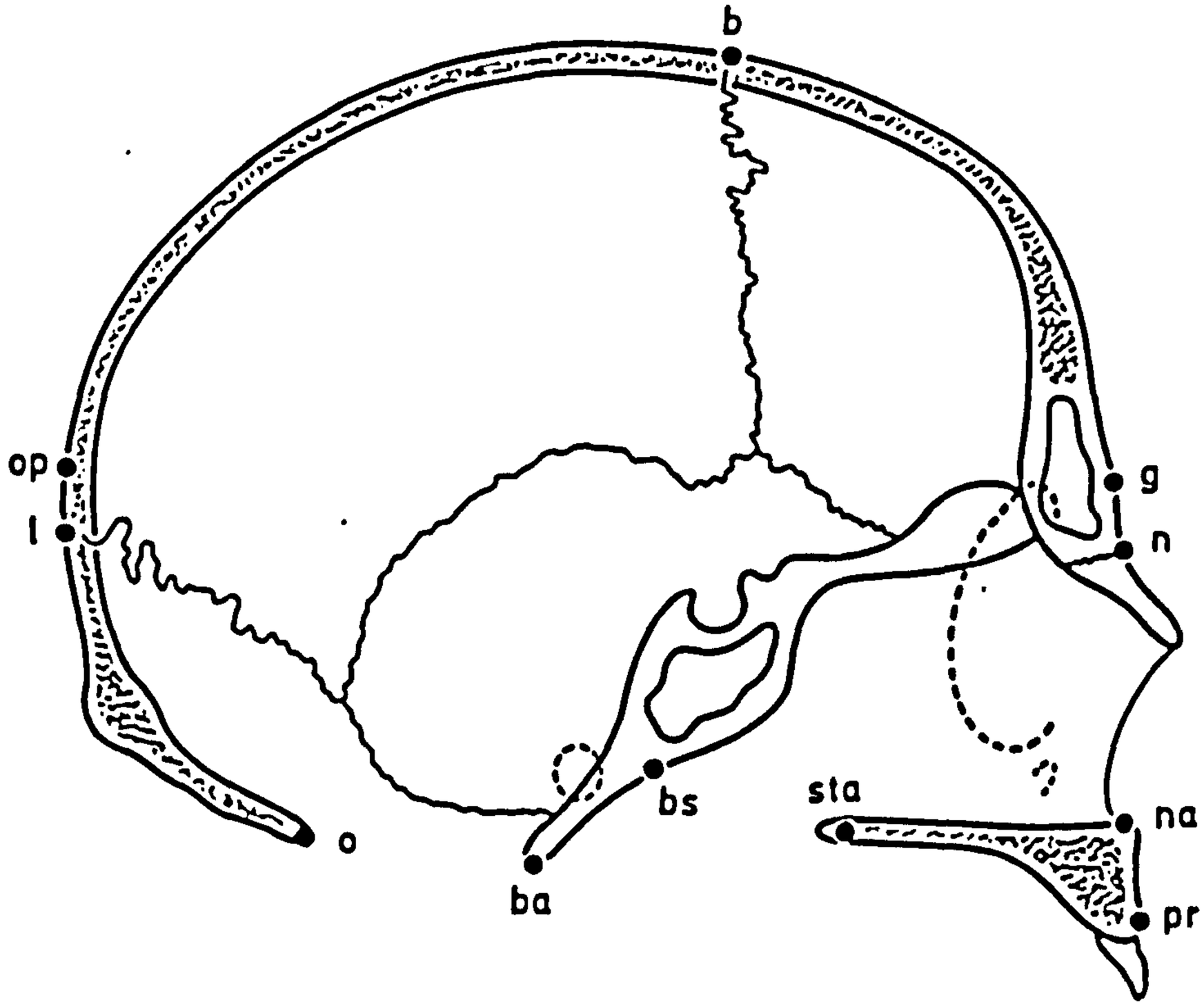



Fig 2.10

definition is given in table 2.2. Using a magnetic digitising tablet, the X,Y co-ordinates of each of the craniometric landmarks was recorded to an accuracy of 1mm.

The method used to calculate the Sneath Dhs is described in the appendix to his 1967 paper (section A3.4). It should be noted that the final equations in this appendix contain an algebraic error insofar as the square root signs are inappropriately placed. Calculation of Dh in this study followed a corrected method.

A matrix of mean inter-group Dh's was calculated and each element was divided by the pooled within group standard deviation of Dh's. This had the effect of standardising the intergroup Dh matrix such that the distances were now expressed in S.D.U.

*Precision of measurement*

Errors of measurement of the x,y co-ordinate pairs have the effect of increasing $D_h$. This effect is most significant when comparing two nearly identical shapes. Sneath (1967), discussed the effects of measurement error, he estimated that a 1% error in the location of the landmarks on each diagram would result in a Dh of 0.0566 instead of zero for identical shapes.

Five sagittal tracings were taken from each of five chimpanzee and five human crania. For each skull the mean value of Dh taken between the ten combinations of the five tracings was calculated. In each case it was less than 0.0566 and on average was 0.0267, well below the value estimated for a measurement error of 1%.

*Effects of size*

The method of Sneath compensates for differences in absolute size by re-expressing the original X,Y co-ordinates as x',y' which are standardised in relation to the dispersion of landmarks about the centroid, Xmean,Ymean. This results in a Dh of zero for forms which are identical in shape independent of size. No account is taken of the effects of allometry.

This method of "size correction" is similar, but not identical to an adjustment made on the basis of area. This leads to a theoretical problem in comparing the

pattern of group dispersions with that obtained from the other methods in this study (see "Definition of size"–above). In practical terms such comparisons are unlikely to be greatly misleading. Shape differences far outweigh size differences in the groups examined (again see above).

d) Normative shape factors

Four shape factors were calculated from each outline. They are described by Exner (1978), each one expresses some aspects of shape, e.g. undulation of outline, elongation, aspect ratio, etc. In the case of a circle each would equal 1 and tend to zero as the measured property deviates from the state encountered in a circle.

The four shape factors were calculated from the following equations:

1. $$F_1 = \frac{4.\pi.A}{P^2}$$

2. $$F_2 = \frac{P - \sqrt{P^2 - 4.\pi.A}}{P + \sqrt{P^2 - 4.\pi.A}}$$

3. $$F_3 = \frac{4.A}{\pi.D^2max}$$

4. $$F_4 = \frac{Dort}{Dmax}$$

where:

A = Area enclosed by the boundary

P = The boundary perimeter

Dmax = The maximum diameter

Dort = The maximum diameter at right angles to Dmax

F1 and F2 are measures of undulation of the outline, as the enclosed area decreases relative to the perimeter they become smaller. It is to be expected that these two measures are highly correlated, however F2 is more "sensitive" than F1, and the process of calculating Mahalanobis' distances takes due account of the effects of correlation. F3 is a measure of shape elongation as is F4. F3, unlike F4 which is simply the aspect ratio of the shape, considers the relationship between the area and the maximum diameter, producing data which express a slightly different aspect of form.

*Method of measurement*

The shape factors, unlike the three preceding approaches to measurement, were calculated independently of the need to identify homologous landmarks except those which, in this study, were used to delineate the boundary between neuro– and viscero– cranium, the nasion and the basion.

Each tracing was modified such that the foramen magnum and the nasal aperture were "closed" by a straight line connecting the bony extremes, the posterior border of the nasal septum was projected into the midline when asymmetrical. In order to allow consideration of neurocranial and viscerocranial proportions as well as whole skull shape, factors were calculated from three outlines for each skull – viz. the whole tracing, a tracing of the viscerocranium, and a tracing of the neurocranium. The neuro–viscerocranial boundary was taken as the line connecting the nasion and the basion.

The projections were digitised such that the x,y co–ordinates of a series of points 1mm. apart on the outline were recorded. From each digitised outline the area A, the perimeter P, the maximum diameter, Dmax, and the maximum

diameter orthogonal to Dmax, Dort were calculated. These were used to calculate the series of 4 shape measures from each of the three outlines, 12 factors per skull.

*Precision of measurement*

An analysis of variance of the indices was carried out using data calculated from the five chimpanzee and five human crania. In each case the errors of measurement were insignificant relative to the variation encountered between the crania ($p < 0.01$).

*The effect of size*

Each of the shape factors is a dimensionless quantity and as such size has no influence on them (subject to the considerations furnished by Atchley, Gaskins and Anderson, 1976, and Albrecht, 1978a, and reviewed earlier in this chapter).

e) Fourier analysis

This method (based upon polar co-ordinates) is of use where the outline is closed and contains no re-entrants so that only one point on the outline is intersected by any one radius.

The length of each radius at angle θ from the start point, can be calculated as a function of θ;

$$f(\theta) = a0 + \sum_{n=1}^{127} an.\cos n\theta + bn.\sin n\theta$$

where;

a0...an = the cosine components

and

b0...bn = the sine components (b0 = 0 and is therefore omitted).

Each sine and cosine component is an expression of an aspect of shape, and has the same units as the units of the polar series (length). The first cosine component, a0, is a measure of overall size, related to the square root of the area enclosed by the outline. The absolute value of each component is governed by the locations of the centroid and the startpoint, a series of amplitude coefficients can be calculated from the sine and cosine components:

$$A_n = \sqrt{a_n^2 + b_n^2}$$

where:

$A_n$ = the amplitude components

$a_n$ & $b_n$ = the cosine and sine components respectively

The amplitude components are unaffected by location of the start point, and as such were calculated as a means of assessing its influence on the results obtained using the sine/cosine representation. The amplitude coefficients alone do not allow reconstruction of the form; this can be achieved in conjunction with their complements, the phase lag angles calculated by:

$$\Phi_n = \mathrm{Tan}^{-1}(-b_n/a_n)$$

where:

$\Phi_n$ = the phase lag angles

$a_n$ & $b_n$ = the cosine and sine components respectively

This study has followed common practice (e.g. Lu, 1965, Lestrel, 1974 and Johnson *et al.*, 1985) in concentrating on a statistical analysis of the sine/cosine series. The amplitude coefficients were studied independently as a means of assessing the influence of using the prosthion as a start point for the Fourier series.

*Method of measurement*

The mid sagittal tracing of each skull was digitised using a magnetic tablet, this produced a series of x,y co-ordinate pairs, 1mm apart, over the whole outline. Between 350 and 550 pairs of co-ordinates were recorded from each, and these were used to calculate 256 polar co-ordinates at equiangular intervals, centred around the calculated centre of area of the tracing. The polar series was derived such that angular displacements were recorded anticlockwise with reference to the line joining the prosthion and centroid. Following equalisation of areas the 256 polar co-ordinates were submitted to a Fourier analysis. 128 Fourier coefficients were calculated, each Fourier coefficient comprising a sine and cosine component.

*Precision of measurement and selection of components*

The errors produced by the measurement process might be expected to be concentrated in those coefficients which describe fine undulations, i.e. the higher order coefficients. For this reason the derivation of some coefficients might be expected to be unreliable. These can be considered to contain a large element of measurement error or "noise". The calculation of the generalised distance matrix as applied by many workers to anthropological data requires that the number of specimens be large relative to the number of variates employed. This study comprised some 300 specimens and in all 255 sine and cosine components were derived.

It is apparent, that for the reasons of eliminating "noisy" data and to allow suitable statistical analysis some compromise between informational content and practicality must be achieved.

An analysis of variance carried out on the components derived from five human crania on five different occasions indicated that all of the first 30 sine/cosine component pairs were accurately measurable ($P<0.001$ in all but 2 cases where $P<0.01$) and that the majority of the other components were also reliable ($P<0.01$), but that the errors of measurement were increasingly significant in the higher coefficients where occasional values of $P>0.05$ were obtained. The human crania were not selected for similarity though they were all of the same racial group. When the same test was applied to data derived from the chimpanzees, which were chosen to be alike as possible, P was $<0.001$ for all but two of the first twenty sine components (sine 12, $P< 0.05$, sine 13, $P<0.01$) and all but one of the first twenty cosine components (cosine 8, $P<0.01$). The higher order components derived from the chimpanzee tracings were less reliably measured than those from the men.

The Fourier coefficients allow the reconstruction of the mid-sagittal projection, the more components used, the better the approximation. Figure 2.8 shows such a series of reconstructions derived with increasing numbers of component pairs. The visual impression improves as more pairs are added to the reconstruction until, after about the first 20 pairs the outline is quite similar to the initial tracing. Adding more data improves the outline in only the finer detail.

An analysis of variance was carried out for each of the 255 components, the between group variance being compared with the pooled within group variance to enquire whether or not each variate showed any significant difference between groups (in all cases $P<0.001$). The variance ratio showed a marked tail off in the higher components, levelling at a value of 5 (d.f. 10 and 288) by the twenty fifth

coefficient pair.

From these simple univariate and visual approaches it seems that between 20 and 25 Fourier coefficients can be measured accurately, allow reasonable reconstruction, and show a significant difference between group means. This was tested by a multivariate assessment of their ability to classify unknown individuals.

A series of ten discriminant function analyses were performed using data from the groups of extant hominoids (table 2.1). In each case 90% of the group members were used to construct a discriminant function, and the remaining 10% were classified using it. For each pair of data files the discriminant function was calculated using increasing numbers of coefficients. This was repeated ten times using a different 10% of the individuals as test data. The results indicated that a minimum of 25.1% of individuals were misclassified (never between species or genera, only between the sexes) when 20 sine ($b_1..b_{20}$) and 20 cosine ($a_1..a_{20}$) components were compounded. The use of this method is fully described by O'Higgins and Williams (1987), and Johnson *et al.* (1985).

On the basis of these tests a data file comprising sine components 1 to 20 and cosine components 1 to 20 was compiled for statistical analysis. Analysis of the amplitude/phase−lag data was also confined to the first 20 pairs, these being derived from the sine and cosine components, and being subject to the same considerations.

*Effects of size*

In order to be consistent with those methods of shape measurement which produce data independent of size all cranial tracings were standardised to the same area. This is reflected in the fact that the calculated value for the first cosine component, $a_0$ varied less than 1% between individuals. The same considerations apply here as to many of the preceding methods of shape measurement, though areas are equal the method of scaling does not allow for allometric effects.

## III. Statistical methods

The data produced by each of four methods of form description (linear and angular dimensions, angles and indices, shape factors, and Fourier analysis) were submitted to univariate and multivariate statistical analyses. The fifth method, the method of least squares, produced no data suitable for univariate study. By nature, it considers the cranium as a whole and results in a distance measure between crania. In this sense it is analogous to the multivariate statistical methods.

### The Development and application of a suite of programs for the statistical analysis of the data

These studies are highly dependent upon a number of statistical techniques. The quantity of data and the degree of sophistication of some of these techniques required the development of a suite of specially designed software for the tasks of data collection, checking, transformation and analysis. The software comprises a series of modules with facilities for data transfer between programs. These programs link with a number of commercially available statistical packages where suitable. The software collection as a whole was named the "Leeds morphometric suite" by the late Professor E.H. Ashton. The suite is shown diagrammatically in fig. 2.11.

Data such as linear and angular dimensions can be entered via a BBC microcomputer. This program offers interactive graphics, and a synthesised speech "readback" of data for checking of entries. An interactive facility allows data

FIGURE 2.11 – Diagrammatic representation of the Leeds Morphometric suite

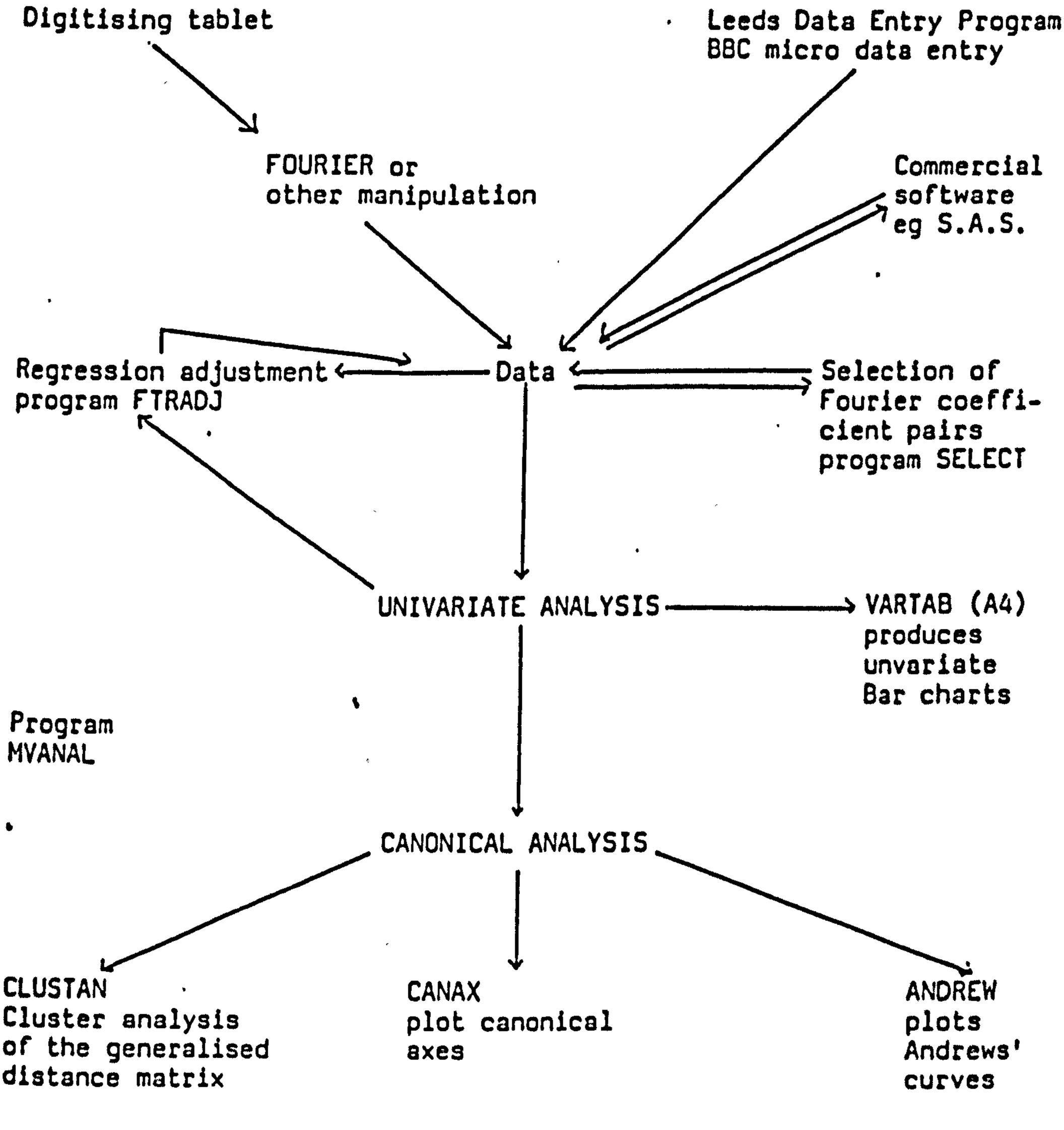



Fig 2.11

transfer to the mainframe for statistical analysis. Outline data in the form of x,y co-ordinate pairs can be collected on a microcomputer via a digitising tablet and transferred to the mainframe for subsequent manipulation. The manipulations applied in this study were Fourier analysis, performed by fast Fourier transform (the program being supplied by Dr. R.M. Flinn) and the calculation of shape factors from simple quantities such as the area and perimeter of outlines. Indices were calculated on the mainframe from the linear and angular dimensions by a one-off program.

The commercial statistical analysis package, SAS, (SAS, 1982) was employed in order to perform the repeated discriminant analyses required in order to determine the optimal number of Fourier coefficients to discriminate between groups. A program SELECT, from the Leeds Morphometric suite reduced the number of Fourier coefficients in the data deck to the required number. The linear and angular dimensions were submitted to regression analysis for certain studies. This was undertaken in the early stages using a program FTRADJ which is a development of one supplied by Dr. R.M. Flinn and in the later stages using S.A.S.

Univariate and some multivariate analyses were carried out using program MVANAL which is a development of a program for canonical analysis written by Dr. R.M. Flinn. This program offers the interactive selection of groups and the interactive selection of univariate studies. Groupwise and variatewise analyses can be undertaken. The equality of within group variances can be examined. The program allows the logging of data when it may be helpful in rectifying discrepancies in variances. A data set with resorted groups can be output in a suitable format for regression adjustment by program FTRADJ. The data required

in order to plot univariate bar charts is output once group variances have been equalised. Program VARTAB can be called later in order to construct these and to relay them to a graph plotter for drawing. A matrix of correlations between variables can be produced by the final part of the univariate analysis sections of MVANAL.

Program MVANAL proceeds to the calculation of Mahalanobis' distances between groups allowing the interactive selection of variables for study. The $D^2$ matrix and its square root, the D matrix, are output, together with a list of nearest linkages between groups to allow the later construction of a minimum spanning tree. The computation of the D matrix has been checked by comparison with that derived from the same data by the discriminant analysis program available within SAS. The matrices agreed to all significant figures. The D matrix is output in a suitable format, together with all the control language necessary to run the commercially available CLUSTAN (Wishart, 1982) cluster analysis package. The job control language initialises such a run after execution of MVANAL.

The Mahalanobis' D matrix is submitted to a principal co-ordinate analysis after the method of Gower (1966) to produce an ordination equivalent to that of canonical axes. The suite offers the user the option of excluding small groups from the calculation of Mahalanobis' distances since these may distort the overall pattern of group separations. If this option has been selected the scores of the small group centroids on the canonical axes are now calculated by use of the variate loading factors for each axis. The group scores on each canonical analysis are output to a file for later plotting by program CANAX or for the computation of Andrews' curves, Andrews (1972), by program ANDREW.

The program terminates after calculating the contribution of each axis and of each original variable to the overall discrimination between groups.

A number of multivariate statistical procedures such as principal component analysis and the later canonical analyses were carried out by submitting the data to analysis using the SAS package.

The documentation, including a fuller description of this suite of programs, and the programs themselves are available for inspection in the Department of Anatomy, University of Leeds.

## Univariate statistical analysis

For each variable from each of the first four methods of form description a mean and standard deviation was calculated.

This first study aimed to compare the overall pattern of contrasts revealed between the extant hominoids by each of the methods of cranial form description. In this context the univariate study was of little value. For each method the ability of each variable to discriminate within and between the groups of men and apes was noted.

Examination of the correlations between variable pairs in all of the original sets of data demonstrated that a significant amount of correlation existed in each. This lack of independence of variables can lead to substantial distortion of the distances calculated between taxa. For this reason multivariate analysis employed Mahalanobis' distances whenever possible.

## Multivariate statistical analyses

### *Should the data be logged?*

In the cases of the linear and angular dimensions, the angles and indices and the shape factors it was noted that the within group variances were frequently unequal. This inequality was such that groups with larger mean values of a particular variable tended to have larger variances. Following the recommendation of Sokal and Rohlf (1969: p382) logging of the data produced generally more equal group variances.

A basic assumption in the calculation of the Mahalanobis' distance is that within group variances are equal. It might be expected that deviations from this assumption should result in a distortion of the apparent group relationships. Past experience from the studies of the Birmingham School has indicated that the methods are robust, and that minor deviations from this rule have little effect on the observed pattern of group distribution. This was further tested as a preliminary to this study. The structures of the minimum spanning trees calculated from raw, partially logged (logging only those variates in which variances are unequal), and fully logged linear and angular dimensions were compared. The partially logged and fully logged data produced identical trees, the raw data differed only in the order of clustering of the male and female chimpanzees with the orangs (the difference in distances required to cause such a change being only 0.25 of an S.D.U. which was equivalent to less than a 2.5% change in distance). The same test was undertaken using raw, partially logged and fully logged angles and indices and shape factors. The logging of data had no effect on the observed pattern of linkage within either of these data sets. The Fourier coefficients showed fewer inequalities of within group variances. The same test when applied to the Fourier coefficients did however result in minor differences in the pattern of linkage of the races of modern man and in the order of linkage of the sexes of chimpanzee.

It was decided, primarily on theoretical grounds, that analyses of linear and angular dimensions, angles and indices, and shape factors would use fully logged data.

*How different are the results obtained using midline data from those obtained using three dimensional data ?*

The linear and angular dimensions were taken between landmarks scattered over the whole of each cranium. The indices, in being derived from the linear and angular dimensions, are also related to the three dimensional morphology of each cranium. This contrasts with the data derived from Fourier analysis and with the shape factors which measured only the form of the mid-line projection of each cranium. The method of least squares produced a matrix of inter-cranial form differences based upon the positions of mid-line landmarks.

The multivariate analysis of the data from extant groups was directed first towards determining the degree to which studies of the midline of crania tend to disagree with those of the full three dimensional structure.

The data files of linear and angular dimensions and of angles and indices were each subdivided into three subsets. The first contained all the data from the mandibles and crania, the second the data from the cranium alone, and the third the data from the mid-line projection alone. The six resultant data files were each submitted to multivariate analysis. A matrix of Mahalanobis' distances between group centroids was calculated from each data file. Additionally Mahalanobis' distances were calculated from the midline variables taken from the file of scaled linear and angular dimensions.

Differences in the patterns of phenetic group relations demonstrated by 3 and 2 dimensional data were quantified by calculating correlations between the distance matrices.

*How different are the results obtained by different methods of cranial form description?*

The next part of this study concentrated on assessment of differences in the patterns of between group phenetic relationships and the discriminating power demonstrated by the data derived from the different methods of measurement. These two aspects are related but not identical.

I shall briefly detail the selection and statistical analysis of the data produced by each method of measurement.

Scaled data is used throughout unless otherwise stated. This allows a more sensible comparison of techniques.

*Linear and angular dimensions*

After scaling the dimensions from each cranium (by ratio with respect to the square root of the midline area) a subset of 25 dimensions and angles from the midline projection was taken. Two of the points which were projected on the mid-sagittal craniograms were used to take two projected dimensions. These were the porion (used to measure projected auricular height) and the infra-orbital foramen position (used to measure projected basi infra-orbital length). Though these are not strictly midline measures they were included amongst the midline data because they were taken from the cranial tracing and used one point which lay on the midline. Comparison of results obtained from data including these dimensions with results from data omitting them showed no appreciable difference.

The 25 variables were used to calculate a matrix of between group Mahalanobis' distances. A histogram of distances was drawn, the average distance between groups was calculated and a minimum spanning tree was constructed.

The usefulness of these linear and angular dimensions in identification problems was assessed by repeated discriminant analysis. The data file was divided into two, the first subset consisted of the data from a randomly selected 10% of individuals, the second contained the data from the remaining 90%. The larger file was used to construct discriminant functions between groups. The data in the second file were classified in accordance with these derived functions. The analysis proceeded by selecting repeated tenths and by going through the whole process until all the individuals had been included in the smaller file. The total number of misclassifications was recorded.

*Angles and indices*

The 17 angles and indices from the midline were selected for each cranium. These were used to calculate Mahalanobis' distances between groups. The distance matrix was then used to draw a histogram of between group distances and to construct a minimum spanning tree. The average between group distance was calculated. The data were then submitted to a repeated discriminant analysis in the same way as were the linear and angular dimensions in order to determine their utility in identification.

*Method of least squares*

It has been noted earlier that Sneath's method of least squares allows the calculation of a matrix of average between group distances. Each element was divided by the pooled within group standard deviation of Dh's in order to reexpress the distances in S.D.U. Average between group distances were calculated, a histogram of between group distances and a minimum spanning tree were drawn. Repeated discriminant analysis was not possible.

*Shape factors*

In all, 12 shape factors were calculated from the midline projection of each cranium. Four of these were calculated from the whole outline, four from the neurocranium and four from the viscerocranium. Two files were created, one containing all 12 variables, the other containing only the four from the whole cranial outline.

Between group Mahalanobis' distance matrices were calculated from each file. From both matrices the average between group distance was calculated and a histogram of between group distances was drawn. From the distance matrix calculated using all 12 variables a minimum spanning tree was constructed. All twelve variables were used in a repeated discriminant analysis similar to that used for the linear and angular dimensions and the angles and indices.

*Fourier analysis*

Fourier data in the form of the amplitude/phase–lag coefficients and sine/cosine coefficients were studied. The sine/cosine series was used to construct a graphical representation of the mean cranial outline for each group.

The selection of the first 20 pairs of sine/cosine coefficients by a criterion of discrimination has already been detailed in the section dealing with measurement methods. The percentage of crania misclassified by each repeated discriminant analysis was plotted against the number of variates used in each analysis. The curve described by these points shows a minimum between 18 and 20 variate pairs. It was concluded that each cranium was adequately described by 40 variables in all, the sine and cosine components of Fourier coefficients 2 to 21 inclusive. A data file containing these 40 variables from each cranial outline was created.

The file of 40 sine and cosine components was used to calculate a matrix of between group Mahalanobis' distances from which the mean between group distance was calculated, and a histogram of distances and a minimum spanning tree were drawn. A second data file containing the amplitude and phase-lag components of the Fourier series was created. This was used to draw group average power spectra. A subset of these data comprising the first 20 pairs of amplitude/phase lag components was taken and used to calculate between group Mahalanobis' distances. Again, the average distance was calculated and a histogram of between group distances was drawn.

The discriminating ability of each sine and cosine component on its own was assessed by calculating the F-ratio (between group variance relative to pooled within group variance). High values of this ratio reflect good discriminating ability between groups. A bar chart of F-ratio against variate number was drawn. This was used to select increasing numbers of variables for repeated discriminant analysis. This is analogous to the technique used to determine the best 20 sine-cosine coefficient pairs. A graph was drawn of the percentage of individuals

misclassified against the number of "best discriminating variables" used. This whole procedure was undertaken in order to optimise the discriminating ability of the data in multivariate combination.

The Fourier data so far examined are start point dependent. Errors in the location of the start point will affect the whole series. For this reason a data file containing only the first 20 amplitude coefficients was used to calculate a matrix of between group Mahalanobis' distances. In common with the other sets of analyses the mean distance was calculated, a histogram of distances and the minimum spanning tree were drawn.

*Comparison of the results obtained from each set of data*

Each method of analysis resulted in a distance matrix from most of which (detailed earlier) a histogram of distances was drawn, the average distance was calculated, and the minimum spanning tree was constructed. These results can be directly compared.

A further comparison was undertaken by treating each distance matrix as if it were simply a list of observations taken on each method. This allowed the calculation of correlations between distance matrices. A principal component analysis of the correlation matrix between distance matrices was performed.

The relative utility of each method in problems of identification can be assessed by observing the number of misidentified individuals from the repeated discriminant analysis of the data produced by each measurement method.

# RESULTS

## A. Univariate analyses

In the context of this first study the results of univariate analysis are of little interest. No measurement obtained by one method of description is directly comparable with those obtained by the others. Common to the data from all of the methods some variables showed little between group variation, others clearly differentiated the apes from the men, and others showed contrasts within apes and humans.

The Fourier data allowed a number of novel comparisons. From the sine–cosine series average group outlines were reconstructed using the mean value of each variable. These are presented in fig. 2.12.

The amplitude–phase lag series is a mathematical transformation of the sine–cosine series. Amplitude component n indicates the amplitude of the wave of order n. Examination of the relative magnitudes of the amplitude components allows the frequency characteristics of an outline to be investigated. Plots of successive amplitude components (power spectra) for the apes and men are presented in figures 2.13 – 2.15. All of the power spectra show a peak for the second order component (indicating bilobedness) which is greater for apes than men and larger for males than females. The orangs are uniquely distinguished from the chimpanzees, gorillas and men in showing a smoother tail off. The other groups show a levelling or slight rise in the magnitude of amplitude components 5 and 6.

FIGURE 2.12 – Group mean outlines reconstructed from the sine–cosine Fourier series

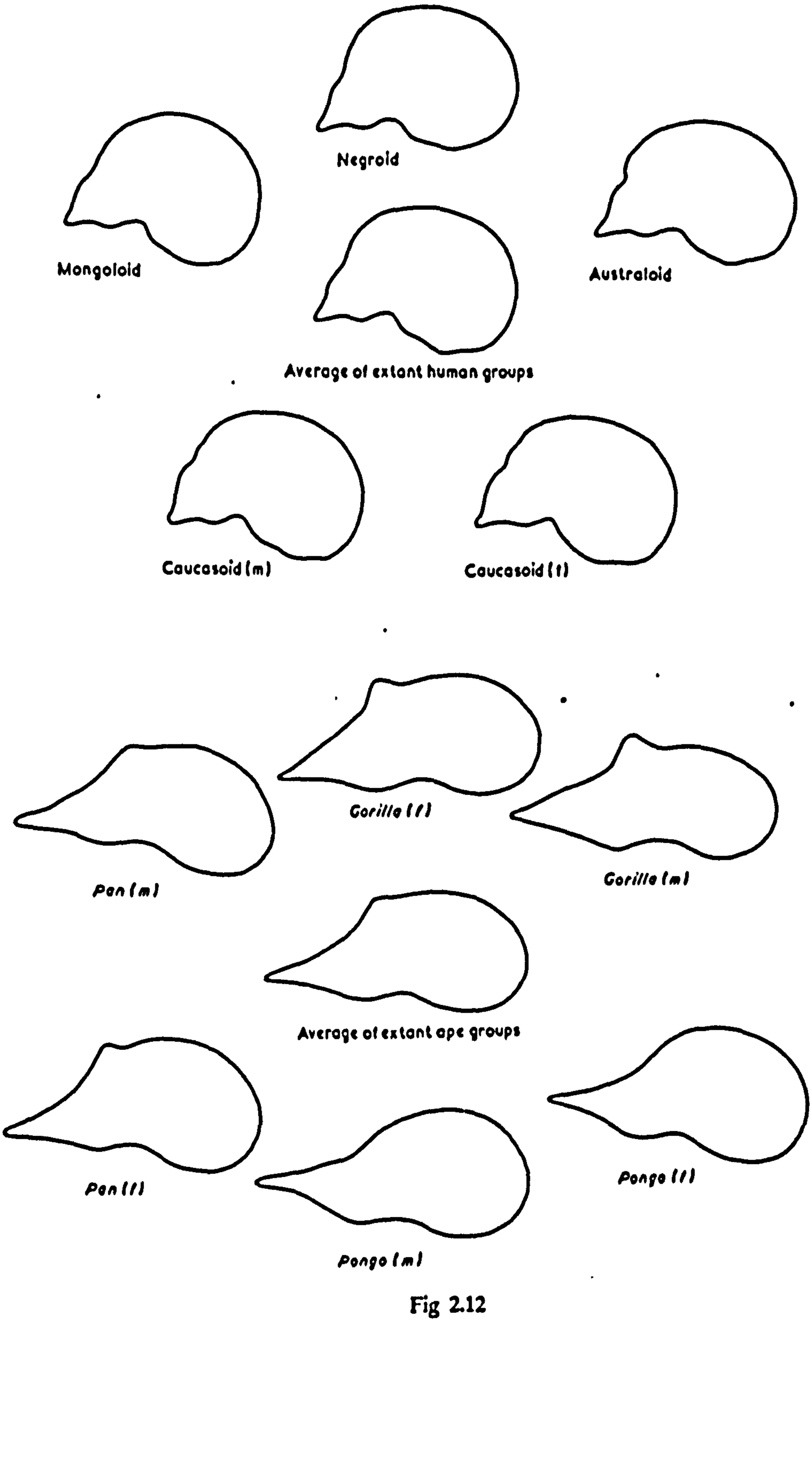



Fig 2.12

FIGURE 2.13 – Power spectrum for *Pongo* and *Pan*

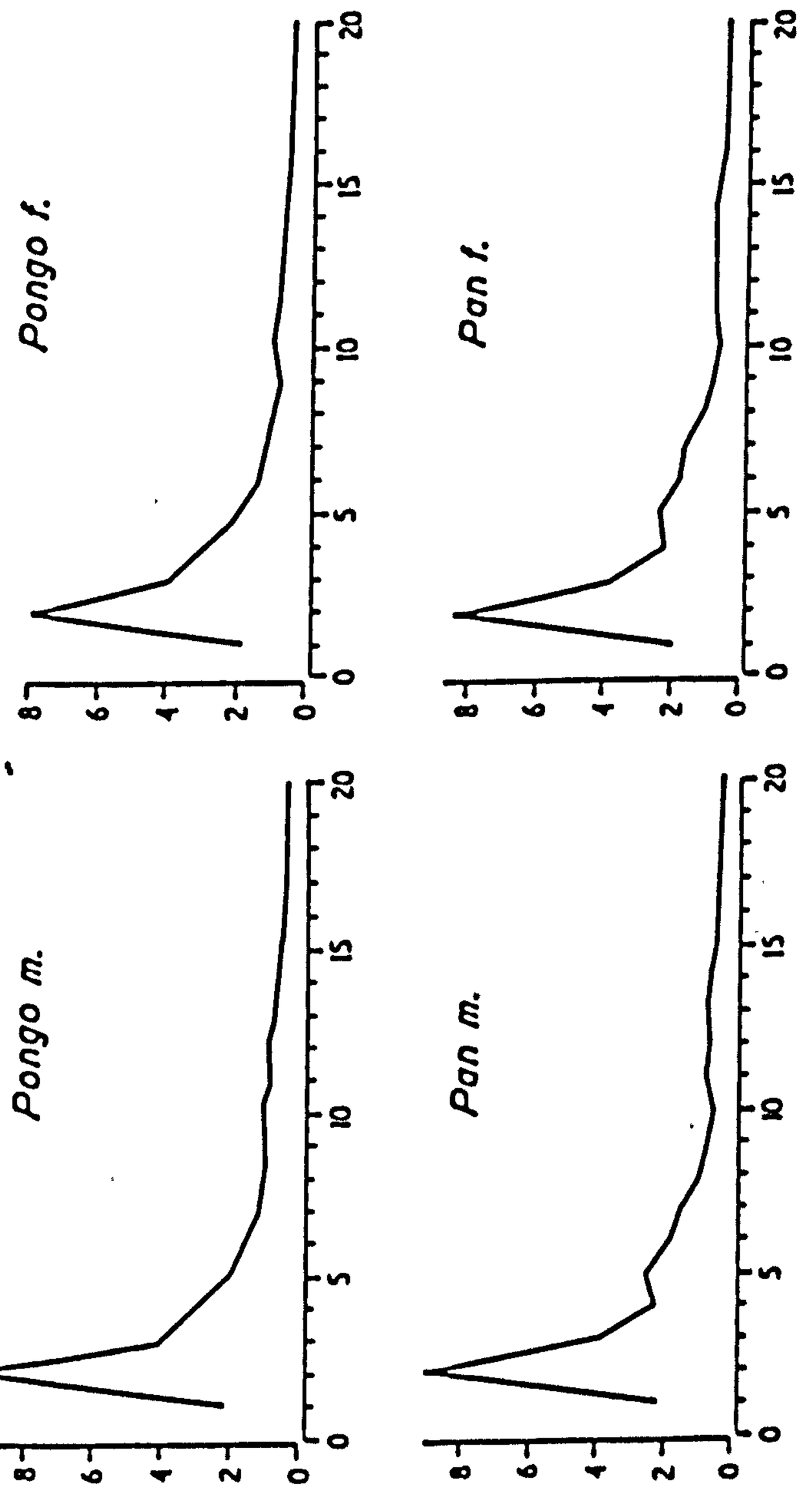



Fig 2.13

FIGURE 2.14 – Power spectrum for *Gorilla* and the average ape power spectrum +/_ 90% confidence limits

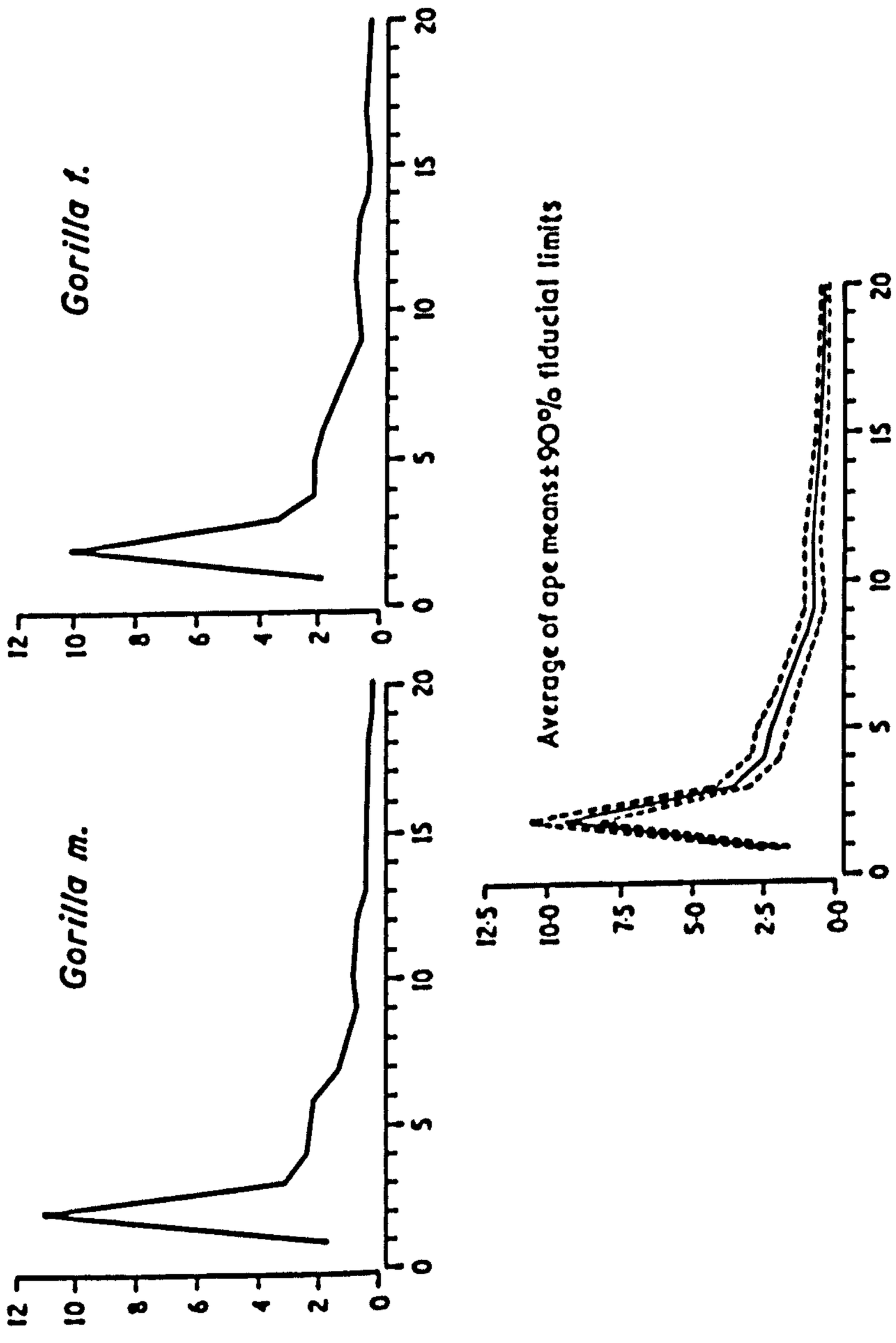



Fig 2.14

FIGURE 2.15 – Power spectrum and average power spectrum +/_ 90% confidence limits for the groups of *Homo*

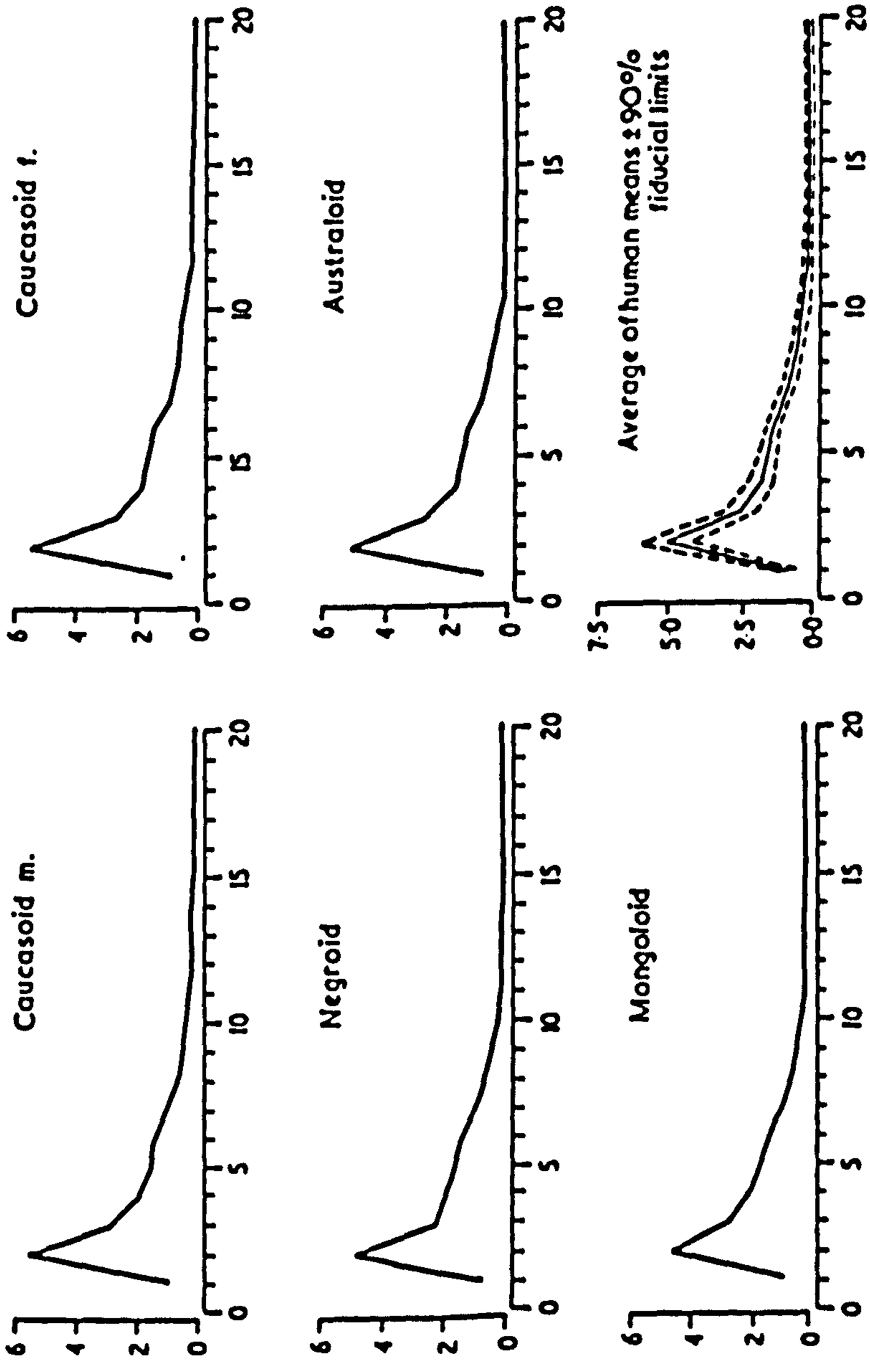



Fig 2.15

## B. Multivariate studies

### 1. Differences between the results obtained using midline data and those from three dimensional data

Only the files of linear and angular dimensions and angles and indices contained data taken from the whole of each skull.

#### Linear and angular dimensions

The mean (between group) Mahalanobis' distance differed between analyses. The study of all 59 linear and angular dimensions from the upper face, braincase and mandible gave a mean distance of 18.84 S.D.U., 34 linear and angular dimensions from the upper face and braincase, 16.1 S.D.U., 25 midline variables, 14.17 S.D.U. and when scaled by ratio for the square root of the midline projection of each cranium, 13.10 S.D.U. The scale of between group separations is affected by the number of variables and by size differences.

Consistent with this are the results of repeated discriminant analyses (table 2.5). Data from the whole skull allows a larger proportion of individuals to be correctly identified than does the data from the midline. Scaling of the midline data further reduces the number of correct identifications.

Table 2.6 lists the correlations between the distance matrices calculated using each of four data sets: (59 linear and angular dimensions from the whole skull, 34 linear and angular dimensions from the upper face and braincase and 25 raw and scaled variables from the midline projection). In no case is this correlation

## TABLE 2.5

Numbers of specimens correctly classified by discriminant analysis of data from 299 individuals

| Measurements | No correctly classified | No incorrectly classified |
|---|---|---|
| 59 raw linear and angular dimensions | 261 | 38 |
| 25 raw linear and angular dimensions | 237 | 62 |
| 25 scaled linear and angular dimensions | 227 | 72 |

## TABLE 2.6

Correlations between studies

| STUDY | | A | B | C | D |
|---|---|---|---|---|---|
| | A | 1 | | | |
| | B | .998 | 1 | | |
| | C | .994 | .996 | 1 | |
| | D | .992 | .989 | .983 | 1 |

A = 59 lin. and ang. dims – whole skull
B = 34 lin. and ang. dims – whole skull less mandible
C = 25 raw lin. and ang. dims – midline
D = 25 scaled lin. and ang. dims – midline

less than 0.98.

These results indicate that the scope of the data (3-d or 2-d) and size differences affect the scale but not the pattern of between group separations.

## Angles and indices

The results obtained by studying angles and indices from the whole skull, the upper face and braincase, and the midline were compared in a similar manner to those derived from linear and angular dimensions. The mean Mahalanobis' distance between groups calculated from 65 angles and indices derived from the upper face, braincase and mandible was 18.06 S.D.U., from 29 angles and indices from the upper face and braincase, 14.21 S.D.U. and 17 angles and indices from the midline, 11.95 S.D.U. The pattern of reduction in mean intergroup distance is similar to that observed from studies of linear and angular dimensions.

On the whole, the mean intergroup distance is less when calculated from angles and indices than from linear and angular dimensions taken from the same anatomical region. This, to some extent, reflects differences in the number of variables used in each analysis. However, in the studies based upon data from the whole cranium more indices were used than linear dimensions yet the mean intergroup distance is less. The indices did not show more intercorrelations than the linear dimensions. The smaller intergroup distances may well reflect the less size dependent nature of indices.

Differences in the pattern of group relationships demonstrated between the full and more restricted data were investigated by calculating the correlations between the distance matrices derived from each. The results are presented in

table 2.7. Reducing the anatomical scope of the data does not significantly alter the observed pattern of group relationships. This result is in keeping with that obtained from the studies of linear and angular dimensions.

TABLE 2.7

Correlations between studies

| STUDY | | A | B | C |
|---|---|---|---|---|
| | A | 1 | | |
| | B | .996 | 1 | |
| | C | .995 | .992 | 1 |

A = 65 angles and indices - whole skull
B = 29 angles and indices - whole skull less mandible
C = 17 angles and indices - midline

## 2. Differences in the results obtained by different methods of cranial form description

### The extent of group separation and the ability to identify individuals of unknown provenance

The Mahalanobis' distance matrices calculated from the scaled midline data derived by each method of description and the shape distance matrix calculated by Sneath's method of least squares are presented in tables 2.8 and 2.9. The mean intergroup distances calculated from these matrices are presented in table 2.10. The largest mean intergroup distances are produced by the analyses based upon linear and angular dimensions and the sine–cosine Fourier series taken from the midline. The smallest are produced by the amplitude Fourier coefficients and the four shape factors taken from the whole outline. These last two methods of shape description are the ones which are least dependent upon the identification of homologies.

Direct comparisons of the mean intergroup distances are likely to give rise to some confusion if they are used to estimate the relative discriminating power of each method of measurement in identification problems. The number of variables submitted to multivariate analysis also influences the intergroup separation. A better assessment of the relative discriminating abilities of the methods is given by reference to table 2.11 which details of the number of individuals misclassified by repeated discriminant analyses.

Figure 2.16 illustrates the way in which the percentage of misclassified individuals changes with the inclusion of more sine–cosine Fourier components.

## TABLE 28

**Mahalanobis' distances calculated using scaled data where appropriate**

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 5.940 | | | | | | | | | |
| Pan m. | 12.250 | 8.810 | | | | | | | | |
| Pan f. | 11.950 | 8.660 | 1.860 | | | | | | | |
| Gorilla m. | 13.830 | 13.920 | 10.870 | 10.870 | | | | | | |
| Gorilla f. | 12.460 | 10.320 | 6.410 | 6.660 | 6.380 | | | | | |
| Caucasoid m. | 23.760 | 19.250 | 17.780 | 17.480 | 22.030 | 18.700 | | | | |
| Caucasoid f. | 23.430 | 19.150 | 17.560 | 17.210 | 21.810 | 18.480 | 3.300 | | | |
| Negroid | 22.700 | 18.270 | 16.720 | 16.410 | 20.800 | 17.720 | 5.170 | 4.780 | | |
| Mongoloid | 23.410 | 19.050 | 17.880 | 17.470 | 21.620 | 18.650 | 4.840 | 4.030 | 3.290 | |
| Australoid | 22.810 | 18.350 | 16.850 | 16.390 | 21.240 | 17.360 | 5.030 | 5.180 | 2.440 | 3.830 |

Mahalanobis' distances: 20 sin/cos Fourier coefficients

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 5.880 | | | | | | | | | |
| Pan m. | 8.350 | 7.050 | | | | | | | | |
| Pan f. | 8.180 | 6.750 | 1.680 | | | | | | | |
| Gorilla m. | 11.310 | 11.300 | 8.470 | 8.620 | | | | | | |
| Gorilla f. | 8.810 | 8.090 | 6.470 | 6.850 | 5.420 | | | | | |
| Caucasoid m. | 20.480 | 17.670 | 16.350 | 16.270 | 18.640 | 17.450 | | | | |
| Caucasoid f. | 18.820 | 17.180 | 15.940 | 15.780 | 18.120 | 16.980 | 3.900 | | | |
| Negroid | 18.520 | 16.640 | 14.470 | 15.290 | 18.880 | 16.680 | 5.400 | 4.840 | | |
| Mongoloid | 19.930 | 16.910 | 15.830 | 15.740 | 18.620 | 17.250 | 4.640 | 4.610 | 3.320 | |
| Australoid | 19.100 | 16.130 | 14.950 | 14.730 | 18.830 | 16.370 | 5.620 | 5.380 | 2.870 | 3.830 |

Mahalanobis' distances: 20 amp/phl Fourier coefficients

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 4.930 | | | | | | | | | |
| Pan m. | 6.800 | 5.760 | | | | | | | | |
| Pan f. | 6.530 | 5.300 | 1.510 | | | | | | | |
| Gorilla m. | 7.310 | 6.660 | 7.300 | 6.170 | | | | | | |
| Gorilla f. | 6.740 | 6.960 | 5.380 | 5.820 | 4.380 | | | | | |
| Caucasoid m. | 11.410 | 9.100 | 9.110 | 8.910 | 11.230 | 9.030 | | | | |
| Caucasoid f. | 11.390 | 9.810 | 9.660 | 9.480 | 11.490 | 9.630 | 1.710 | | | |
| Negroid | 13.340 | 1.110 | 10.320 | 10.030 | 12.850 | 10.060 | 3.350 | 3.030 | | |
| Mongoloid | 12.930 | 10.420 | 10.660 | 10.400 | 13.430 | 10.300 | 2.700 | 2.700 | 1.930 | |
| Australoid | 12.420 | 10.200 | 9.920 | 9.700 | 12.110 | 10.070 | 2.750 | 2.800 | 2.030 | 2.130 |

Mahalanobis' distances: 20 amplitude Fourier coefficients

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 4.840 | | | | | | | | | |
| Pan m. | 6.820 | 5.630 | | | | | | | | |
| Pan f. | 6.870 | 5.170 | 4.130 | | | | | | | |
| Gorilla m. | 8.270 | 6.210 | 8.870 | 6.070 | | | | | | |
| Gorilla f. | 8.410 | 5.470 | 4.490 | 4.390 | 4.100 | | | | | |
| Caucasoid m. | 16.100 | 13.760 | 15.870 | 11.880 | 15.640 | 13.600 | | | | |
| Caucasoid f. | 16.220 | 13.940 | 12.490 | 12.210 | 15.870 | 13.860 | 3.170 | | | |
| Negroid | 14.880 | 12.460 | 11.180 | 11.060 | 14.710 | 12.770 | 4.500 | 4.040 | | |
| Mongoloid | 15.260 | 12.900 | 11.800 | 11.350 | 15.110 | 13.050 | 3.710 | 3.500 | 3.000 | |
| Australoid | 14.870 | 12.520 | 11.380 | 10.960 | 14.670 | 12.680 | 3.720 | 3.440 | 3.700 | 3.380 |

Snoath's shape distance

## TABLE 29

**Mahalanobis' distances calculated using scaled data where appropriate**

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 8.800 | | | | | | | | | |
| Pan m. | 9.950 | 7.030 | | | | | | | | |
| Pan f. | 10.140 | 6.900 | 1.730 | | | | | | | |
| Gorilla m. | 10.550 | 10.930 | 9.500 | 10.630 | | | | | | |
| Gorilla f. | 10.583 | 9.170 | 5.570 | 6.630 | 5.513 | | | | | |
| Caucasoid m. | 21.690 | 18.570 | 17.160 | 16.920 | 22.270 | 19.610 | | | | |
| Caucasoid f. | 22.620 | 19.280 | 17.880 | 17.580 | 23.063 | 20.130 | 2.320 | | | |
| Negroid | 13.870 | 16.540 | 15.720 | 15.240 | 21.380 | 18.380 | 6.660 | 6.330 | | |
| Mongoloid | 20.340 | 17.810 | 17.030 | 16.630 | 22.610 | 19.523 | 3.630 | 3.630 | 3.260 | |
| Australoid | 20.620 | 16.960 | 15.550 | 15.150 | 21.200 | 18.050 | 6.160 | 6.180 | 2.870 | 3.930 |

Mahalanobis' distances: 25 linear and angular dims.

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 4.160 | | | | | | | | | |
| Pan m. | 8.690 | 6.040 | | | | | | | | |
| Pan f. | 8.740 | 5.690 | 1.520 | | | | | | | |
| Gorilla m. | 8.870 | 10.010 | 8.720 | 8.810 | | | | | | |
| Gorilla f. | 8.310 | 8.010 | 5.080 | 5.890 | 4.600 | | | | | |
| Caucasoid m. | 21.200 | 18.060 | 16.030 | 15.690 | 2.510 | 18.200 | | | | |
| Caucasoid f. | 21.730 | 18.610 | 16.540 | 16.110 | 22.030 | 18.740 | 1.870 | | | |
| Negroid | 19.450 | 16.230 | 14.030 | 14.220 | 20.630 | 17.310 | 4.010 | 3.540 | | |
| Mongoloid | 20.390 | 17.310 | 15.640 | 15.260 | 21.490 | 18.180 | 3.240 | 2.960 | 2.880 | |
| Australoid | 19.060 | 16.860 | 14.820 | 14.390 | 20.360 | 17.140 | 3.630 | 3.190 | 2.210 | 3.420 |

Mahalanobis' distances: 17 angles and indices

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 3.710 | | | | | | | | | |
| Pan m. | 3.880 | 4.930 | | | | | | | | |
| Pan f. | 3.920 | 4.070 | 1.390 | | | | | | | |
| Gorilla m. | 8.730 | 8.340 | 7.060 | 7.300 | | | | | | |
| Gorilla f. | 8.530 | 8.730 | 3.730 | 4.700 | 3.730 | | | | | |
| Caucasoid m. | 16.390 | 14.790 | 14.630 | 14.280 | 17.790 | 15.040 | | | | |
| Caucasoid f. | 15.870 | 14.190 | 14.190 | 13.820 | 17.310 | 15.290 | 1.510 | | | |
| Negroid | 14.550 | 12.380 | 13.350 | 12.910 | 16.470 | 14.640 | 3.440 | 4.430 | | |
| Mongoloid | 18.010 | 14.240 | 14.870 | 14.240 | 17.380 | 13.770 | 2.810 | 2.880 | 3.320 | |
| Australoid | 14.530 | 12.710 | 12.870 | 12.380 | 16.240 | 14.230 | 4.660 | 4.030 | 2.460 | 3.400 |

Mahalanobis' distances: 12 'shape factors'

| | Pongo m. | Pongo f. | Pan m. | Pan f. | Gorilla m. | Gorilla f. | Caucasoid m. | Caucasoid f. | Negroid | Mongoloid |
|---|---|---|---|---|---|---|---|---|---|---|
| Pongo f. | 2.310 | | | | | | | | | |
| Pan m. | 2.280 | 0.960 | | | | | | | | |
| Pan f. | 2.760 | 1.270 | 0.530 | | | | | | | |
| Gorilla m. | 1.580 | 2.360 | 2.230 | 2.680 | | | | | | |
| Gorilla f. | 2.080 | 1.730 | 1.260 | 1.670 | 1.200 | | | | | |
| Caucasoid m. | 14.020 | 12.350 | 11.970 | 11.300 | 13.300 | 12.950 | | | | |
| Caucasoid f. | 13.510 | 11.860 | 11.520 | 11.060 | 13.000 | 12.120 | 1.070 | | | |
| Negroid | 12.150 | 10.450 | 10.210 | 9.780 | 11.730 | 10.810 | 2.980 | 2.030 | | |
| Mongoloid | 13.310 | 12.250 | 11.830 | 11.480 | 13.410 | 12.470 | 1.460 | 0.850 | 2.100 | |
| Australoid | 12.610 | 10.940 | 10.640 | 10.190 | 12.220 | 11.270 | 2.830 | 1.080 | 1.070 | 1.920 |

Mahalanobis' distances: 4 'shape factors'

## TABLE 2.10

Mean distances between modern groups calculated from scaled midline data

| | |
|---|---|
| linear and angular dims. | 13.10 |
| angles and indices | 11.95 |
| 12 shape factors | 10.25 |
| 4 shape factors | 7.28 |
| 20 sin/cos. Fourier coeffs. | 13.92 |
| 20 amp/phl. Fourier coeffs. | 12.43 |
| 20 ampl. Fourier coeffs. | 7.83 |
| Sneath's Method | 9.54 |

All distances except Sneath's $D_h$ are Mahalanobis' D

TABLE 2.11

Numbers of specimens correctly classified by discriminant analysis of midline data from 299 individuals

| Measurements | No correctly classified | No incorrectly classified |
|---|---|---|
| 17 logged angle & indices | 218 | 81 |
| 12 logged normative shape factors | 205 | 94 |
| 20 pairs of sin/cos Fourier coefficients | 224 | 75 |
| 30 sin/cos Fourier coeffs with the largest F−ratio | 230 | 69 |
| 25 scaled linear and angular dimensions | 227 | 72 |

Initially, the addition of more data improves the identification procedure, but later, more data "confuses" the process. This is because the higher Fourier coefficients show more random variation.

Figure 2.17 illustrates that some Fourier coefficients are better at discriminating between groups than are others, the F−ratio varies markedly. Figure 2.18 is like figure 2.16, it illustrates the way in which the number of misclassifications changes with the addition of more Fourier data. The differences between these two graphs are due to the manner in which Fourier components were selected for addition to the discriminant analyses. In figure 2.16 they were added in order of their frequency. In figure 2.18 they were added according to their discriminating ability as indicated by the results of figure 2.17. The manoeuvre of selecting components by discriminating ability resulted in more

correct classifications from Fourier data. This better classification was obtained using less variables than those selected by serial addition: the curve fitted to the points of figure 2.18 levels out at about 30 variables whilst the first 40 variables were selected by serial addition. The advantage of using the first 40 variables is simply that these allow reconstruction of the outlines.

Reference to Table 2.11 shows that the 30 Fourier components with the highest F−ratios perform best in the task of identifying individuals of unknown provenance. The scaled linear and angular dimensions perform nearly as well. The first 20 pairs of sine−cosine coefficients perform less well than these two methods, the angles and indices perform less well than the Fourier coefficients and the shape factors are least able to allow accurate identification.

FIGURE 2.16 – Percentage of crania misclassified using increasing numbers of sine/cosine Fourier coefficients

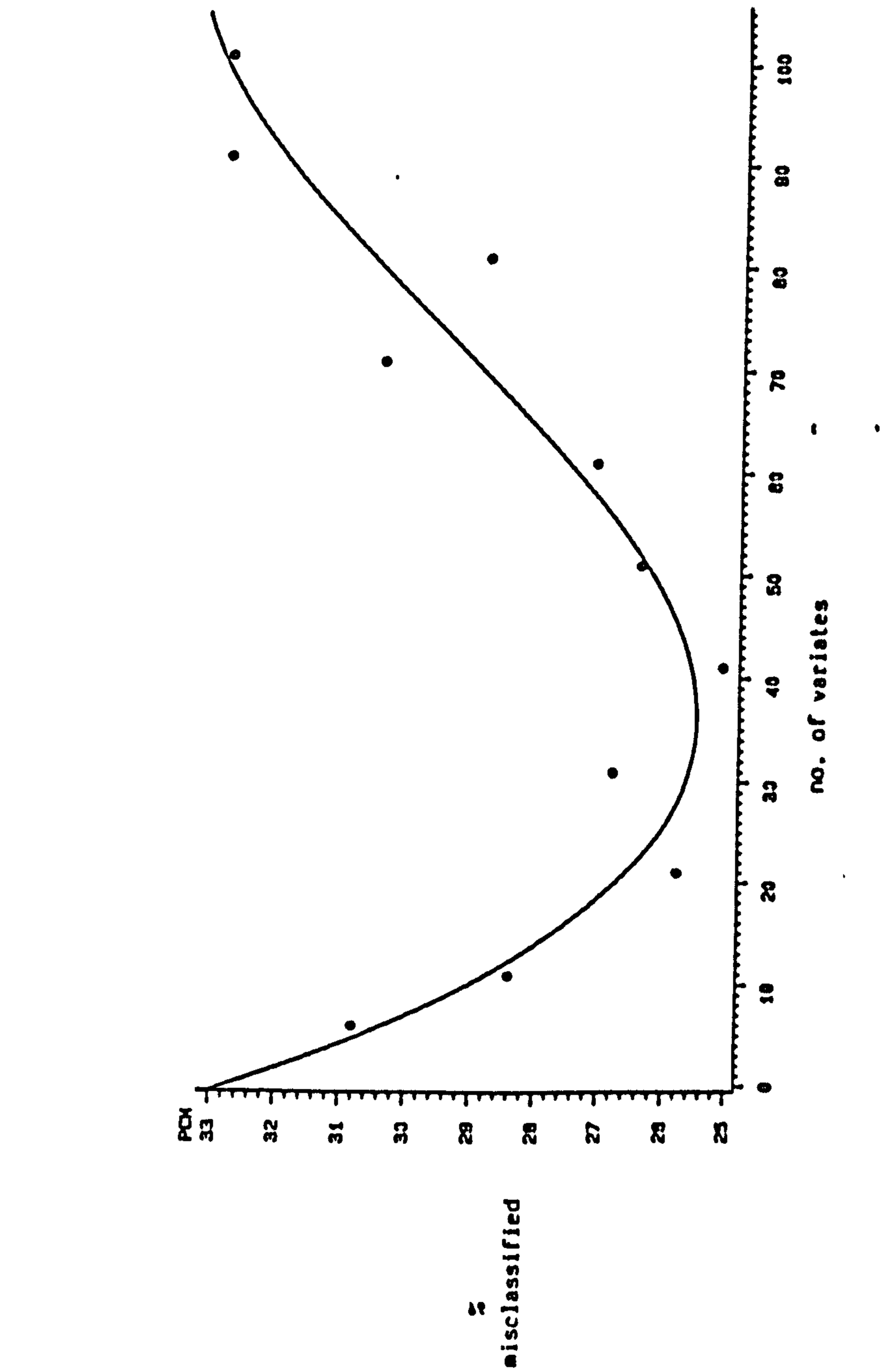



Fig 2.16

FIGURE 2.17 – The discriminating ability of the sine/cosine series of Fourier coeffs. as assessed by the ratio of the between group variance relative to the pooled within group variance (F ratio)

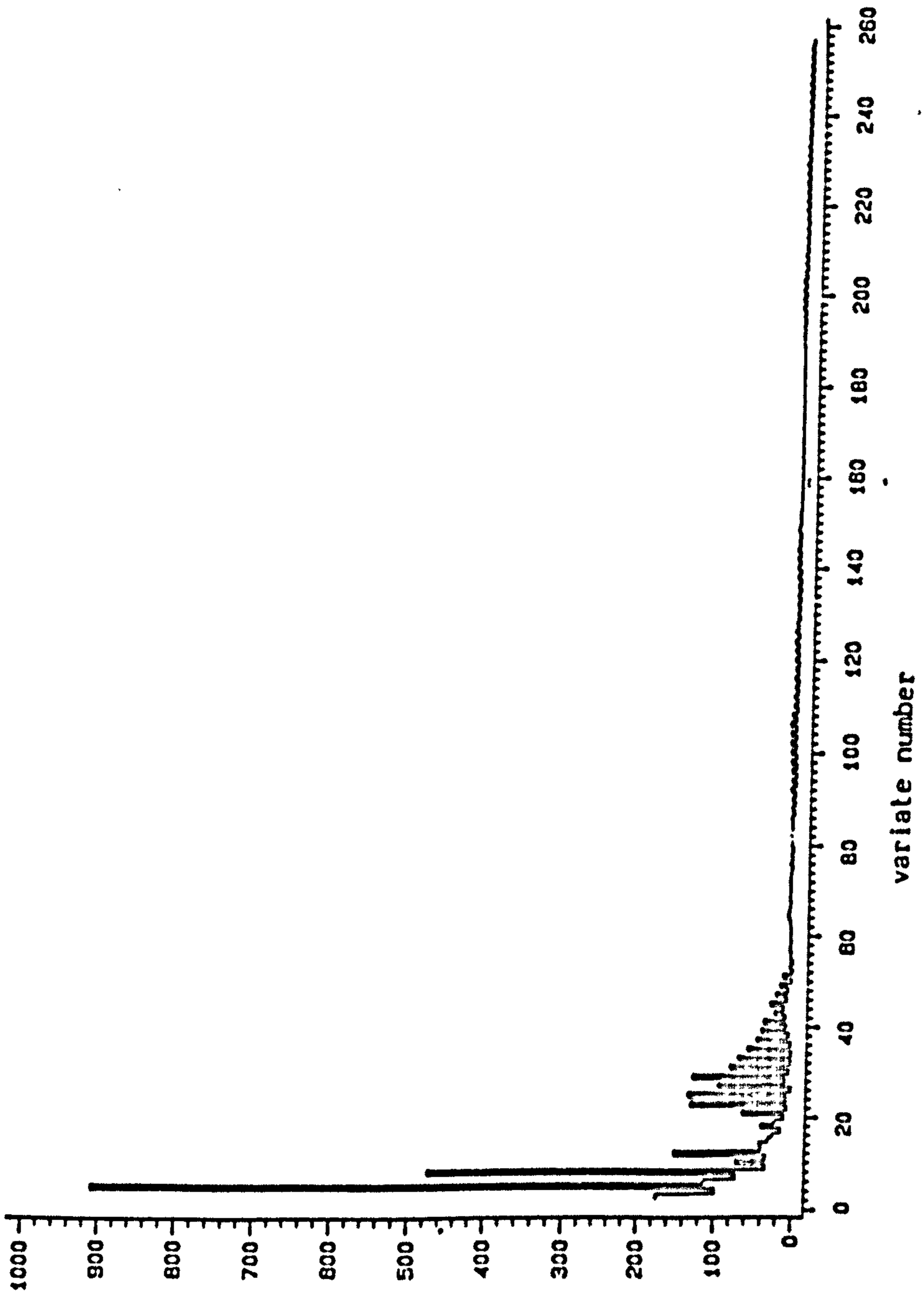



Fig 2.17

FIGURE 2.18 – Percentage of crania misclassified using increasing numbers of variables. Variables are added in order of their F ratios

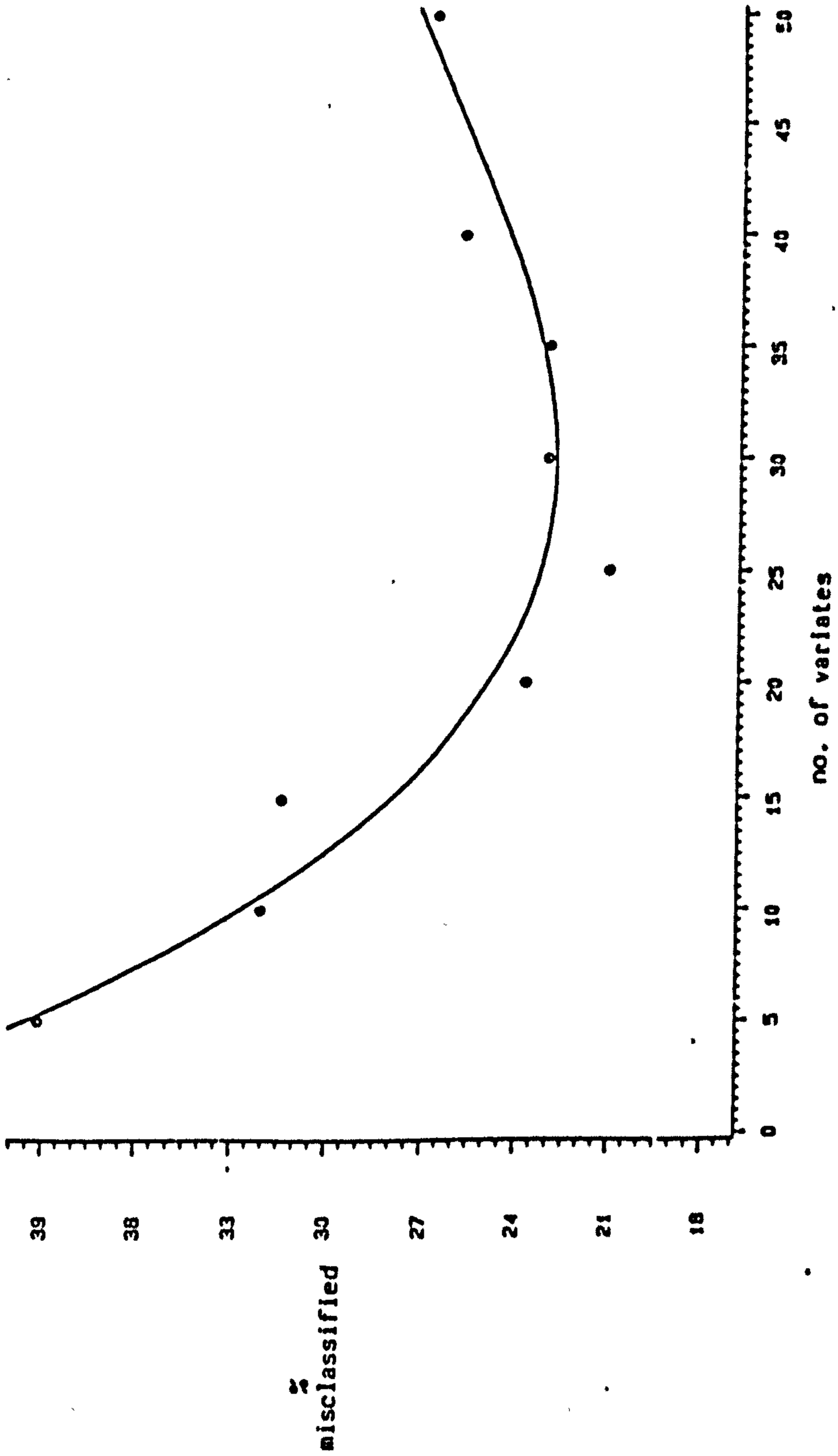



Fig 2.18

Pattern of group dispositions

Histograms of the distribution of distances calculated from the data from each method of shape description were drawn, they are presented in figure 2.19. They all show two major peaks, the first peak is a "low distance peak" and illustrates that all analyses agree that there are some groups which are morphologically similar. The second peak is a "large distance peak" and it results from the common finding that some groups are more different. These common features indicate some agreement in the pattern of group relationships demonstrated by each method.

An attempt was made to study the "structure" of each distance matrix by constructing minimum spanning trees. These are presented in figures 2.20–2.22. All of the methods produce minimum spanning trees in which the apes are clearly distinguished from the men. In all of the minimum spanning trees the sexes of the groups (where sexes are known) are linked together. The scale of each tree reflects the mean distance between groups.

The trees from linear and angular dimensions, angles and indices, Fourier analysis, and the shape factors link the apes in the same way. The chimpanzees are the centre of a "U" shaped cloud, female gorillas link more closely with the male chimpanzees than do female orangs with the female chimpanzees.

The tree drawn from the distance matrix produced by the method of least squares shows a similar pattern of relationships within the apes, however the male chimpanzees are excluded from the "U". The trees from linear and angular dimensions, angles and indices, and Fourier analysis show a more or less spherical cluster of the groups of modern man. The order of clustering is the same:

**FIGURE 2.19 – Histograms of the distribution of distances calculated from the data which result from each method of shape description (data are scaled where necessary)**

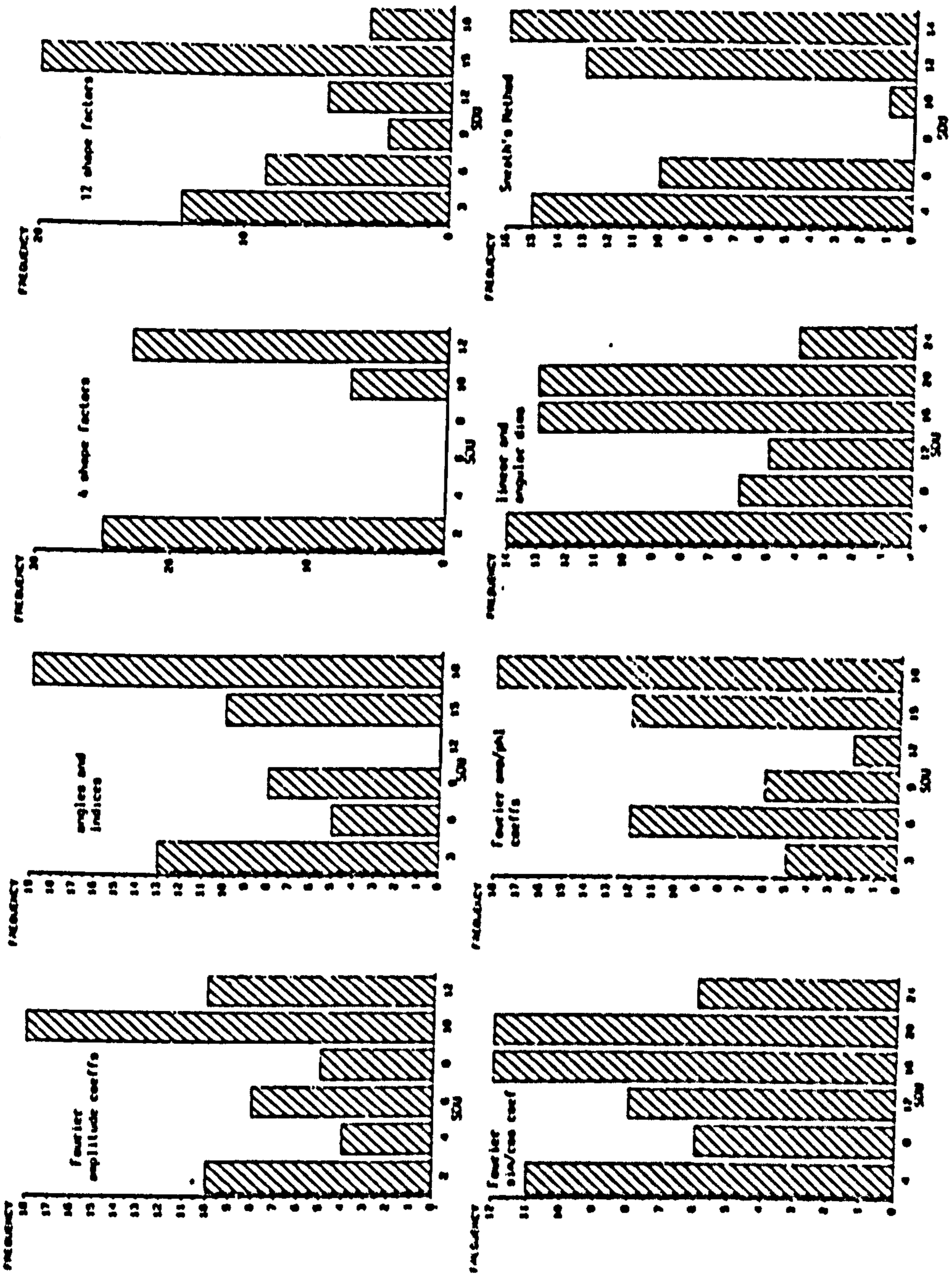



Fig 2.19

FIGURE 2.20 – Minimum spanning trees

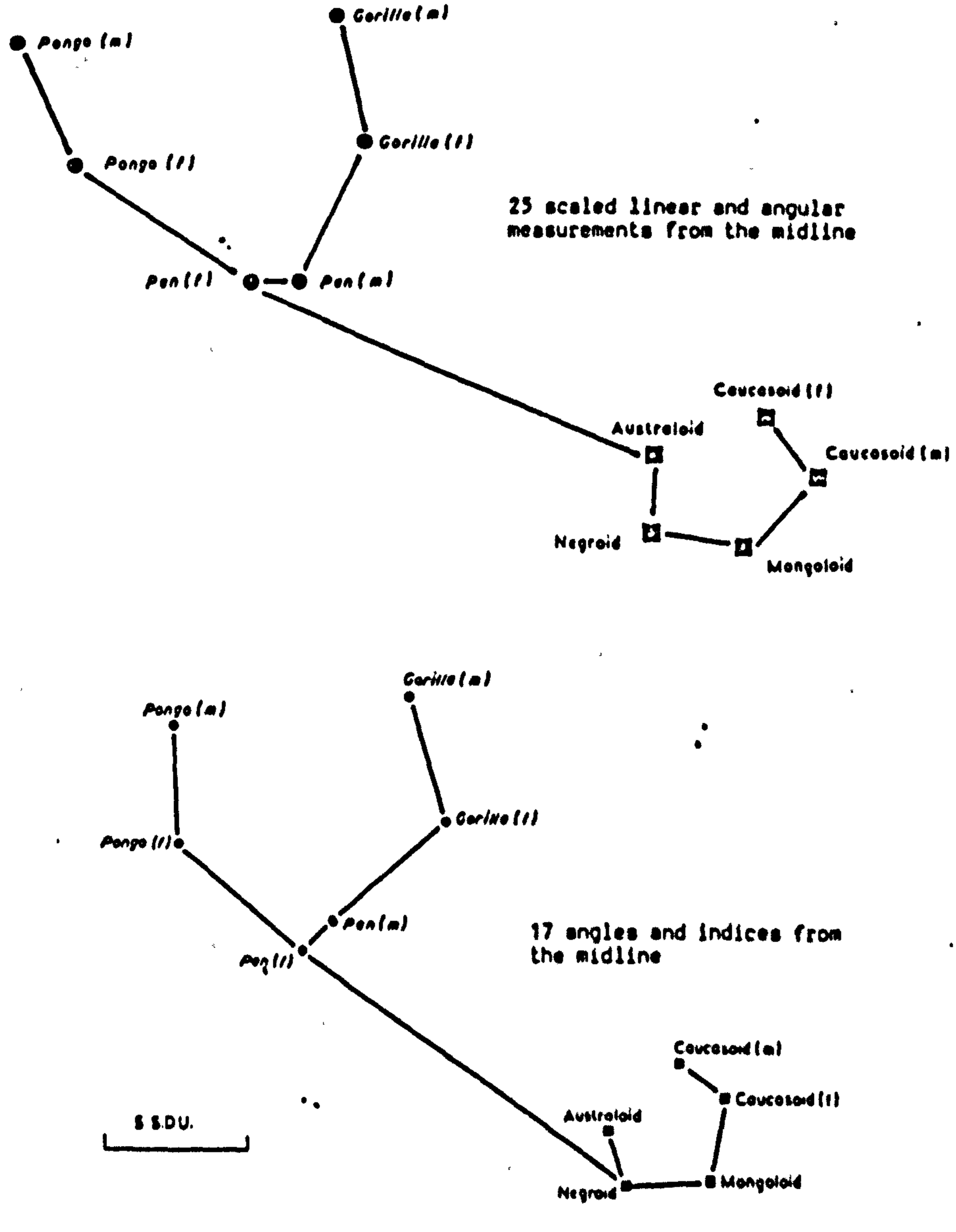
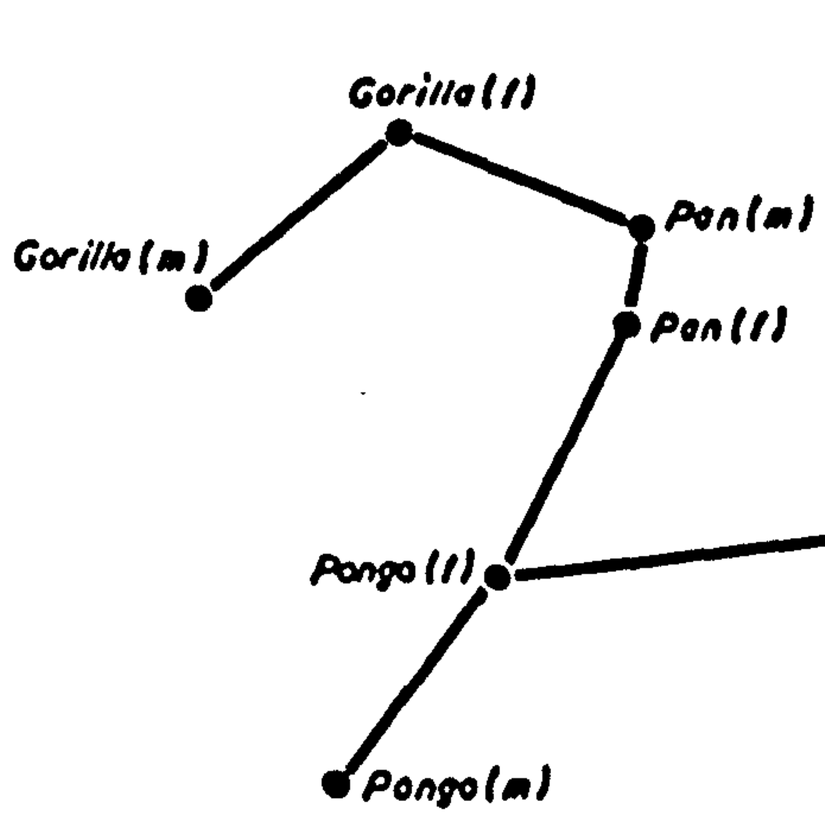
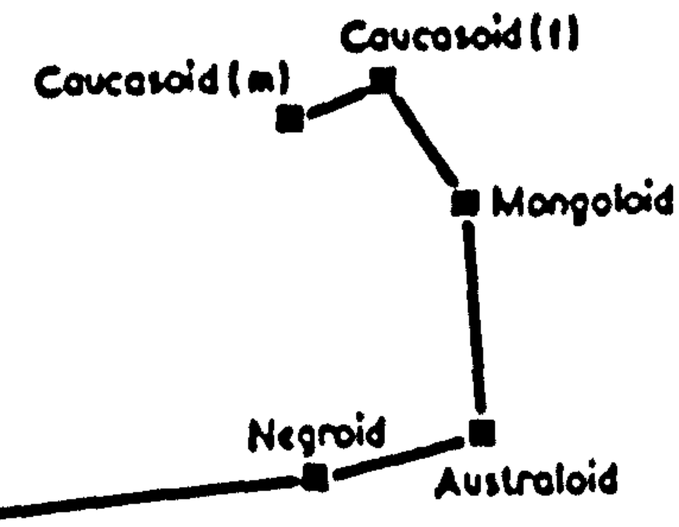


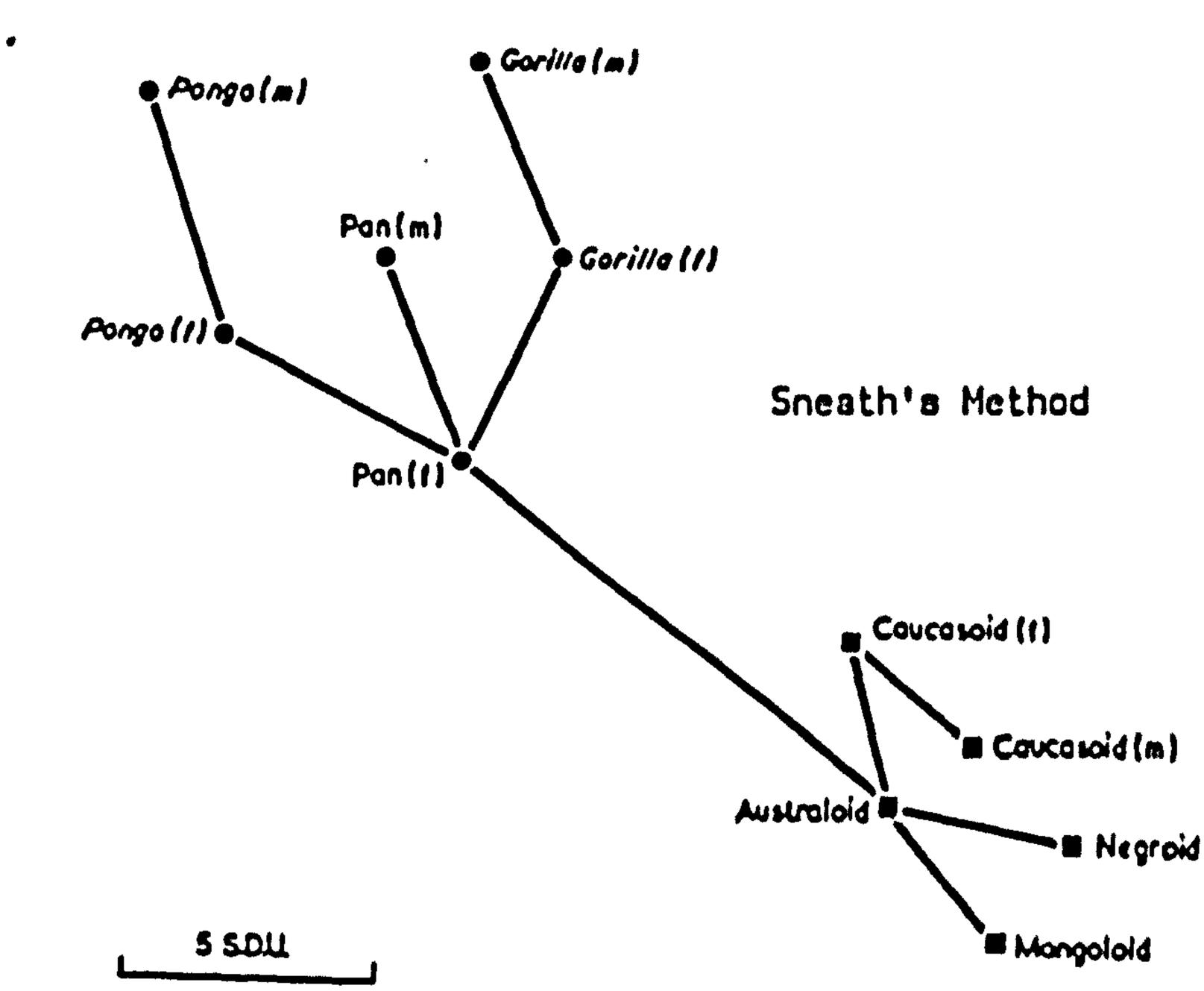

Fig 2.20

FIGURE 2.21 – Minimum spanning trees




12 'shape factors'




Sneath's Method

Fig 2.21

FIGURE 2.22 – Minimum spanning trees

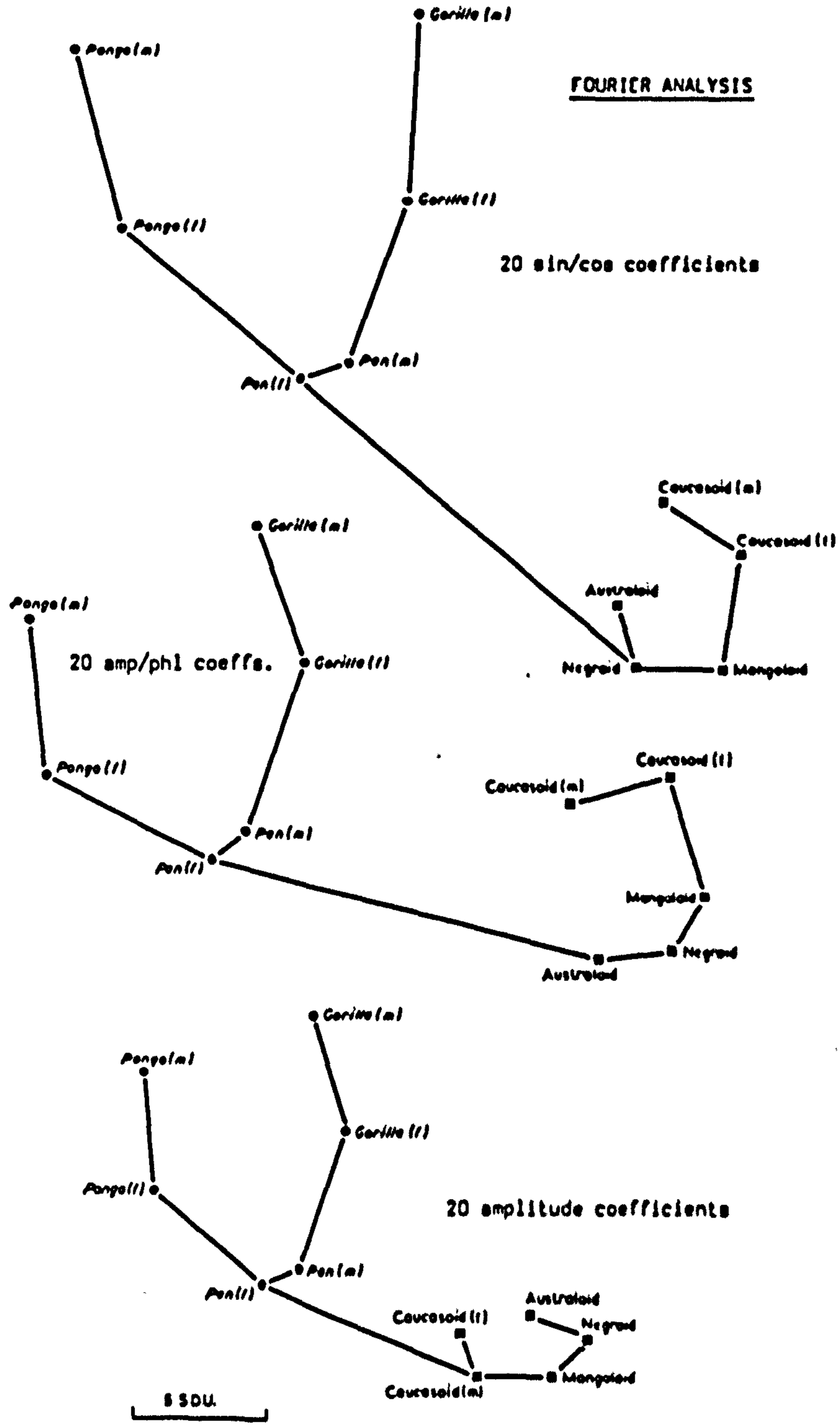



Fig 2.22

caucasoids cluster with mongoloids, which link with negroids, which in turn link with australoids. The trees produced from shape factors and by least squares differ in the exact order of clustering, they do however produce the same spheroidal grouping.

The link between apes and humans is more variable. The angles and indices and the sine–cosine Fourier series produce trees with a long link between negroids and female chimpanzees. The other methods show variation in this linkage. The changes in relative distances required to modify the position of this link are small. This can be confirmed by reference to the distance matrices presented in tables 2.8 and 2.9.

The impression gained from an examination of the minimum spanning trees is that the pattern of group dispositions revealed by linear and angular dimensions, angles and indices, and the sine–cosine Fourier series is similar. The amplitude–phase lag analysis and the amplitude analysis produce patterns which differ slightly from these first three. The shape factors and the method of least squares produce the most dissimilar results.

It should be noted that these differences in result are small compared to the overwhelming agreement between the methods. This can be demonstrated by reference to table 2.12 which lists correlations between the distance matrices produced by each method. All of these correlations are large and they vary little. The methods by and large give similar results with regard to the pattern of group dispositions.

The pattern and scale of group separations produced by each method were further studied by principal component analysis of the correlation matrix between distance matrices. A plot of the first two principal components is presented in figure 2.23.

## TABLE 2.12

Correlations between the distance matrices derived by the studies of scaled data

| | scaled linear and angular dimensions | angles and indices | 12 'shape factors' | Fourier analysis 20 sine/cosine coeffs | Fourier analysis 20 amplitude/phase lag coeffs | Fourier analysis 20 amplitude coeffs | Sneath's Method |
|---|---|---|---|---|---|---|---|
| angles and indices | 0.928 | | | | | | |
| 12 'shape factors' | 0.986 | 0.911 | | | | | |
| Fourier analysis 20 sine/cosine coeffs | 0.988 | 0.924 | 0.967 | | | | |
| Fourier analysis 20 amplitude/phase lag coeffs | 0.994 | 0.929 | 0.984 | 0.993 | | | |
| Fourier analysis 20 amplitude coeffs | 0.907 | 0.854 | 0.892 | 0.913 | 0.904 | | |
| Sneath's Method | 0.981 | 0.914 | 0.973 | 0.966 | 0.977 | 0.863 | |
| 4 'shape factors' | 0.954 | 0.895 | 0.969 | 0.930 | 0.955 | 0.830 | 0.977 |

The extremal positions on axis one are taken up by the distance matrix from 4 shape factors and that from sine–cosine Fourier coefficients. The correlation between the score of a method on this first component and the mean between group distance is 0.996. This first component reflects the scale of the separations demonstrated by each method. The meaning of the higher components is less clear. It is worth noting, however, that positive scores on component two are characteristic of those methods that rely upon a centroid for registration. These are the methods of Fourier analysis and least squares. The lowest score on this axis is that of the 4 shape factors which are the least registration dependent. This interpretation, if correct, demonstrates the relative unimportance of problems of registration in this study.

In figure 2.24 is illustrated a three dimensional plot of the first three principal components from the preceding analysis. This shows more fully the differences between the patterns of group relationships revealed by each method. By far the greatest difference is one of scale as revealed by component one. The differences shown by the other components are smaller and of less certain significance.

FIGURE 2.23 – Plot of the first two principal components derived from the correlation matrix between distance matrices. All data is scaled where applicable.

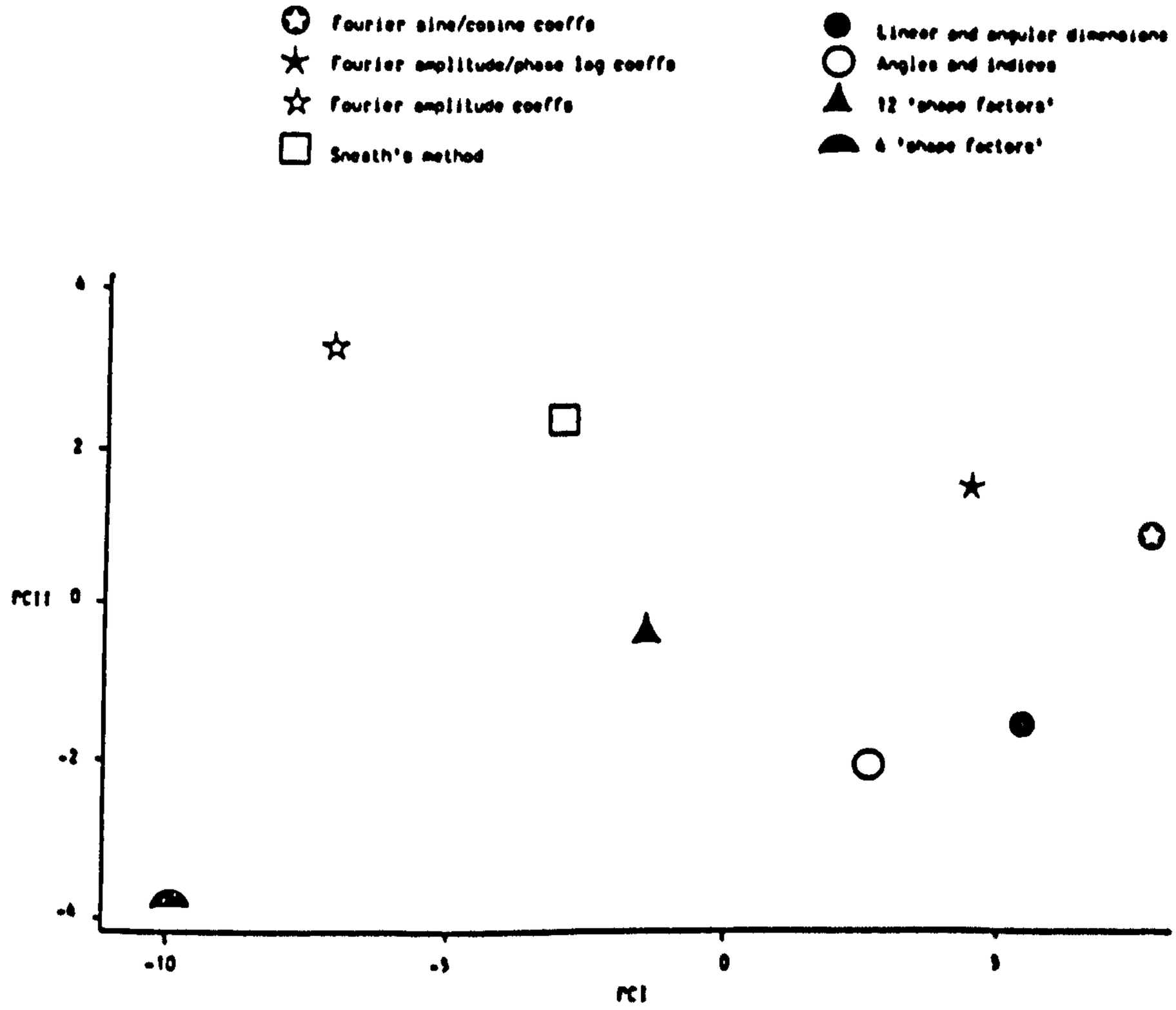
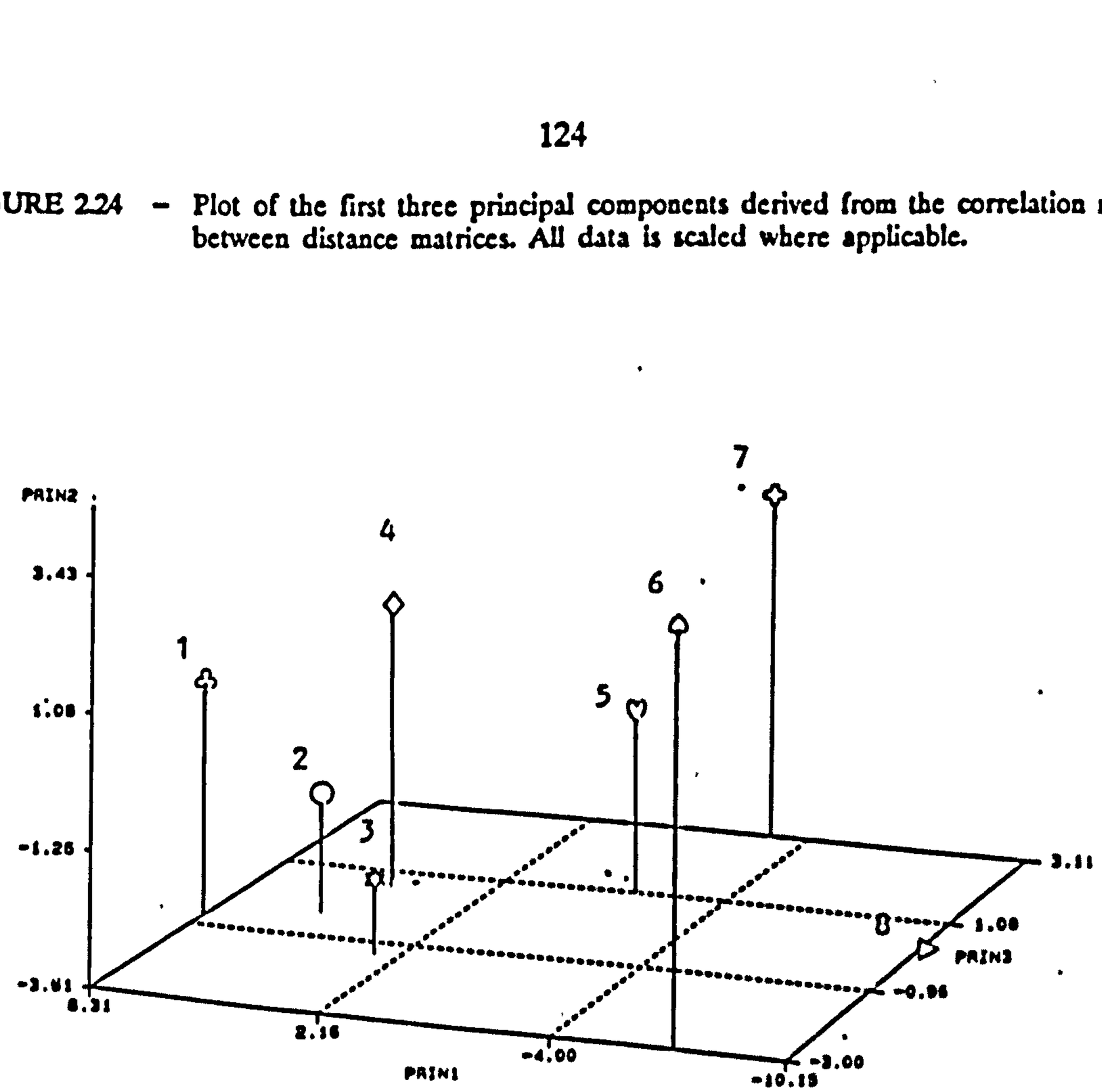



Fig 2.23

FIGURE 2.24 – Plot of the first three principal components derived from the correlation matrix between distance matrices. All data is scaled where applicable.




1. Fourier sine/cosine coeffs
2. Linear and angular dimensions
3. Angles and indices
4. Fourier amplitude/phase lag coeffs
5. 12 'shape factors'
6. Fourier amplitude coeffs
7. Sneath's method
8. 4 'shape factors'

Fig 2.24

# DISCUSSION

In the introduction to this chapter it was stated that the main thrust of the work presented here has been a comparative enquiry into a number of approaches to cranial morphometry. Several of these approaches were only applicable to midline projections of crania. It has therefore been necessary to consider the effect of this reduced anatomical scope on the phenetic relations which are observed between crania before considering the comparative merits of each method.

## 1. Differences between the results obtained using midline data and those from three dimensional data

The results of this study suggest that the pattern of phenetic differences demonstrated between crania by study of midline data does not differ markedly from that based upon three dimensional data. The major difference is in the degree of group separation relative to within group variability.

It seems that the vast majority of factors which influence the shape of the cranium as a whole have a degree of influence on the form of the midline projection. Little "new" information is added by study of parasagittal structures.

Studies of off-midline structures do, however serve to improve the identification of crania of unknown provenance. The inclusion of these data effectively increases the between group variance relative to the pooled within group variance. It is as if the extra data serve to clarify certain features which have only been "hinted at" by the midline studies. This added resolution has little if any influence on the overall pattern of group dispositions.

This result serves as a caution in studies which attempt to treat cranial structures or even dimensions as if they are independent. The development of one structure, it seems, is likely to influence the form of other structures, a finding which is in keeping with modern ideas of pleiotropy.

## 2. Differences in the results obtained by different methods of shape description

This study examined the differences in the pattern and extent of group separations demonstrated by a variety of means of describing midline cranial morphology.

The clearest difference between the results is one of scale of separation. Some methods appear to have provided a "better" (=more complete) description of the form of the midsagittal projection than others. This is reflected in the different numbers of unknown individuals that were correctly identified using each method of shape description. Selected sine−cosine Fourier coefficients and linear and angular dimensions performed best. Angles and indices did slightly worse, shape factors were least reliable. The method of least squares, whilst allowing a classification by minimum distance, was not directly studied in this way.

The methods do produce different patterns of group separation. These differences, at least in the current study, are relatively small in relation to those in the extent of separation. This has been demonstrated by principal component analysis. The differences, as judged by correlations between distance matrices, are slightly greater than those which existed between the two and three dimensional studies of cranial form.

The overwhelming similarities in the patterns of group dispositions which have resulted from the analyses of different types of data are noteworthy because several sets of data included indices (i.e. angles, indices, shape factors and scaled linear dimensions). This similarity in group dispositions occurs despite the cautions furnished by Atchley *et al.* (1976) and Albrecht (1978a). A further finding has been that the effect of registration on the revealed pattern of group separations appears to be minimal.

It seems that, in terms of optimal ability to identify individuals of unknown provenance and in terms of the stability of the pattern of group dispositions, multivariate study of linear and angular dimensions and of the sine–cosine series of Fourier coefficients produce the most effective results. Fourier analysis offers the additional advantage that data collection can be automated (see O'Higgins and Williams, 1987).

It would seem logical to extrapolate from the foregoing study and suggest that: irrespective of the method used to describe cranial morphology in hominoids the resultant pattern of phenetic relationships between OTUs will be stable though there may be some difference in the degree to which OTUs are separated.

The hypothesis that there are no differences in the results of phenetic studies which use any of the data described in this chapter can only be considered to have been partially falsified.

It is prudent, however, to be cautious. The study which has been presented here has used as its material crania of modern men and crania of living hominoids. All of the analyses have agreed that the differences in cranial morphology within the apes and within the men are small relative to the differences between apes and men. In effect, the crania are either of one general

type or another and the pattern of between OTU variation is effectively discontinuous. It is therefore quite possible that the high degree of concordance between analyses is partially a consequence of the limited types of variability in cranial morphology which have been studied. Each method of shape measurement has had to describe a limited range of differences and, in general, each element of the distance matrices calculated from the different data has contained either a large or a small value (consequently matrix correlations are high).

It is quite possible that in situations where differences between all OTUs are larger in relation to the total variability of the sample of OTUs (so there are relatively more "types" of differences to be summarised) the methods will show more disagreement in the pattern of OTU dispositions. A more stringent comparison of the effects of using different methods of cranial form description would include OTUs which differ from each other in a variety of ways and in which the variation between OTUs is more continuous. Such a situation is found within the hominoids when patterns of within group variability or of variability between fossil and extant hominoid OTUs are studied.

Despite this caution the studies of this first chapter have served to permit a practical comparison of the different methods of shape description and a practical test of the usefulness and efficacy of the data generated by each.

3. Comparison of the methods and efficacy of the data

The principal division between the methods employed in this study is that some rely upon the identification of a large number of landmarks whilst others have little or no requirement for landmarks.

In practical terms this means that linear and angular measurements, indices, and the map of landmarks required for the Sneath comparisons are time consuming to collect. There is room for error in the estimation of the position of every landmark and a great deal of time has to be devoted to encoding and checking the data (though the time involved in encoding can be considerably reduced for the Sneath landmark data by the use of a digitising tablet).

By contrast, the shape factors and the Fourier data are derived from tracings of outlines with one or two landmarks marked on each. The collection of the tracings is itself tedious but encoding of data is relatively easy since each outline is simply traced onto a digitising tablet. Recently O'Higgins and Williams (1987) have demonstrated that reasonable results can be obtained by using a video digitiser to extract outline information from standardised cranial photographs. The collection of data using such automated methods can be considerably accelerated and the likelihood of errors in encoding mesurements is greatly reduced.

The data which result from landmark dependent methods of shape description differ fundamentally from these obtained by methods which describe the outline of cranial tracings. Methods which describe the outline give equal weighting to each point whereas landmark dependent methods describe morphology less evenly, giving emphasis to those regions where landmarks are more plentiful. The consequence is that landmark data can be readily related to localised anatomical regions whereas methods which describe the whole outline cannot. Conversely individual linear measurements contain information relating to just the landmarks upon which they are dependent whereas individual shape factors or Fourier components each contain information relating to the whole morphology. The choice of method in any particular study should be influenced by the questions at hand

and the requirements of the investigator.

This study has been directed to an investigation and review of a number of new biometric methods. Their application to the crania of extant hominoids has allowed an appraisal of their relative merits. It seems that studies based upon Fourier analysis and linear and angular dimensions will allow the best description of patterns of cranial variation in terms of providing a maximal separation between OTUs and in producing (at least between the groups studied) a stable phenetic structure. In the following two studies these techniques are used to examine patterns of cranial variation in living and fossil hominoids. The studies allow a more rigorous comparison of these two approaches to cranial morphometry.

# CHAPTER 3

## Patterns of variation of cranial form within certain groups of extant hominoids

# GENERAL INTRODUCTION

The previous chapter compared the relative performance and utility of several approaches to the description of cranial morphology in the primates. From these studies it seems that, at least in studies of extant hominoids, both linear and angular measurements and Fourier data, in multivariate combination, allow a considerable degree of between group discrimination and result in similar overall patterns of between group phenetic relationships.

The studies presented in this chapter have two principal objectives:

first, to allow a further comparison of the relative utility of Fourier data and linear and angular measurements, this time in the context of studies of within–group variability,

second, to examine and compare patterns of within–group cranial variability in certain hominoids (the races of modern man, and chimpanzee, gorilla and the orang–utang).

A further reason for undertaking the studies presented in this chapter is to provide comparative data for the studies of the next chapter, chapter 4, in which patterns of cranial variability within and between certain groups of hominid fossils are considered.

## Patterns of within-group morphological variability

A knowledge of within-group variability is important in any work which attempts to group individual fossils together. Many studies have referred to patterns of within-group variability in extant taxa as a guide to the acceptable limits of variability within proposed fossil taxa (e.g. van Vark, 1984, Chamberlain, 1987, Lieberman *et al.*, 1988).

A significant proportion of the morphological variability within modern hominoids can be attributed to the influence of size on form and to sexual dimorphism (see for example, Wood, 1976, Schmid and Stratil, 1984, Clutton-Brock, 1985, Leutenegger and Cheverud, 1985, Oxnard, 1987). There remains an equally significant component, however, which eludes simple causal explanation. This "random" variation is the result of differences in genotype, environment, diet, and other influences.

An early attempt to use multivariate metrical methods in the determination of the sex (and therefore in the study of sexual dimorphism) of crania is that of Giles and Elliot (1963). These workers used discriminant functions to discern the sex of American white and negro crania. They showed that "discriminant functions based on the two races combined do, for practical purposes, equally well for both races as do those based on and applied to a single race". They concluded from this finding that "the sex discriminant function is employing basic differences and relationships in cranial morphology which are largely independent of racial variation". They further tested their discriminant function on a sample of chimpanzees of known sex and demonstrated that it performed at least as well

as a function derived from the apes themselves. From these studies it seems that there are considerable similarities in the patterns of cranial sexual dimorphism in a wide range of hominoids.

More recently several studies have attempted to describe patterns of sexual dimorphism in the primate cranium and dentition (e.g. Wood, 1975, 1976, Holland, 1986, Uytterschaut, 1986, Oxnard, 1987). A common conclusion is that, amongst the Hominoidea, size differences are in some way related to the shape differences between sexual morphs. The generality of this finding is, however, debatable. In some primate taxa, for instance the bush baby, there appears to be considerable sexual shape dimorphism in the absence of a large sexual size difference (see Oxnard, 1987).

Oxnard (1987) has identified patterns of dimorphism in the variance of certain dental variables. He demonstrates that the chimpanzee, which shows little sexual difference in dental size and shape has a large degree of sexual dimorphism in the variances of certain dental dimensions.

There is some disagreement concerning the variability of patterns of shape dimorphism in hominoids. Wood (1976) in summarising his study stated: "Apart from a few exceptions variables are consistently sexually dimorphic in all groups, differences between primate groups being one of degree of dimorphism rather than due to a different pattern of dimorphism". This finding whilst being consistent with the work of Giles and Elliot (1963) contrasts with that of Oxnard (1987) who found more extensive differences between hominoids in the pattern of dental sexual dimorphism.

Uytterschaut (1986) has reviewed the work of several authors, and has emphasised the importance of size variables in sex diagnosis of human crania.

Her study was directed to a comparison of sexual dimorphism in the crania of different human populations and employed discriminant functions. Her results indicated differences in the vectors of shape difference between the sexes of *Homo* and she concluded that "the construction of a race-independent sex function turned out to be rather difficult, probably because of the differences in the directions of sexual dimorphism factors".

Calcagno (1981) evaluated the general applicability of multivariate discriminant analysis to the sexing of human mandibles. He studied the mandibles of American whites, blacks and Indians and concluded that discriminant functions based upon mandibular dimensions are highly population specific. His study demonstrated a marked reduction in the accuracy of sex diagnosis when intra-group size differences were discounted and he suggested that one reason for the failure of discriminant functions when applied to new populations is the difference in gross size between them. The consequence is that discriminant functions derived from one population will fail on another if the average sizes of males and females within them are different. He suggested that differences in patterns of "human sexual dimorphisms are of little significance in comparison to size variation within the same sex of two populations" in determining the applicability of discriminant functions to different groups.

From this consideration of previous studies of sexual dimorphism it is clear that there is some debate concerning the influence of size on patterns of sexual dimorphism and the degree to which patterns of sexual dimorphism differ between different hominoids and racial groups of Man.

## Aims of the current study

This study aims to further compare measurement techniques, this time in a study of the patterns of cranial variation encountered within extant hominoid taxa. The analyses use both linear and angular measurements and sine–cosine Fourier coefficients. The study provides a comparison of the results obtained using both types of data and of the relative efficacy of each measurement technique in the study of patterns of within–group variability. The relationship between size and sexual dimorphism and differences in patterns of cranial dimorphism between hominoid groups are investigated.

This study further tests the hypotheses that:

1. sine–cosine Fourier data and linear and angular measurements provide similar results in studies of within–group cranial morphological variability;

2. cranial sexual dimorphism is related to sexual size differences in the hominoid groups included in this study;

3. the pattern of cranial sexual dimorphism is identical between the hominoid taxa.

# MATERIALS AND METHODS

## A. Materials

This study employed the 299 skulls of extant hominoids described in Chapter 2 (table 2.1) comprising representatives of the genera *Pan*, *Pongo*, *Gorilla* and *Homo*. The sexes of the ape taxa were known from records, those of the races of mankind with the exception of the caucasoid sample were unknown.

During the course of this study a sample of crania from Hong Kong (Southern) Chinese individuals of known sex (from burial records) became available. It was possible for Professor Moore to visit the Department of Anatomy at the University of Hong Kong to measure the material. He was able to collect a more limited range of measurements from 45 adult crania comprising 16 females and 29 males. These data were used in analyses directed to a comparison of sexual dimorphism in caucasoids and mongoloids.

## B. Methods

In this section I shall describe those metrical and statistical techniques which were applied to the crania of table 2.1. The sample of mongoloid crania which is discussed is that examined in the British Museum. The studies which employed data from the Hong Kong Chinese crania are specifically indicated.

## I. Definition of shape

The shape of each cranium was defined by a series of linear and angular dimensions taken between homologous landmarks (see tables 2.2 and 2.3, data collected by Ashton and Moore) and by Fourier analysis of midline projections. Two further data files were produced, scaled (against the square root of the midline area using ratios and multiplying by a constant) linear dimensions and raw angles, and scaled (equal midline areas) Fourier components. Details of measurement technique and of the selection of the first twenty sine–cosine Fourier coefficient pairs are given in chapter 2.

Thirty one linear and angular measurements from the Hong Kong crania were directly comparable with their counterparts from the larger cranial sample. These common variables are listed in table 3.1.

## TABLE 3.1

**Variables common to the data from Hong Kong Chinese crania and the crania studied in the other parts of this work**

| | |
|---|---|
| 1 | Post – orbital breadth |
| 2 | Maximum cranial breadth |
| 3 | Foraminal breadth |
| 4 | Maximum cranial length |
| 5 | Frontal chord |
| 6 | Parietal chord |
| 7 | Occipital chord |
| 8 | Foraminal length |
| 9 | Auricular height |
| 10 | Basi – bregmatic height |
| 11 | Angle Basion – nasion – bregma |
| 12 | Angle Nasion – bregma – lambda |
| 13 | Angle Bregma – lambda – opisthion |
| 14 | Angle Lambda – opisthion – basion |
| 15 | Angle Opisthion – basion – nasion |
| 16 | Bizygomatic breadth |
| 17 | Orbital breadth |
| 18 | Nasal breadth |
| 19 | Infraorbital breadth |
| 20 | Orbital height |
| 21 | Palatal breadth |
| 22 | Palatal length |
| 23 | Nasal height |
| 24 | Upper facial height |
| 25 | Subnasal height |
| 26 | Angle Bregma – basion – prosthion |
| 27 | Angle Basion – nasion – prosthion |
| 28 | Basi – nasal length |
| 29 | Basi – infraorbital length |
| 30 | Basi – staphylion length |
| 31 | Basi – prosthion length |

## II. Statistical methods

*Univariate studies*

The first part of the univariate study was undertaken in order to detect any sexual dimorphisms in the linear and angular measurements and the sine–cosine Fourier coefficients.

Each of the raw linear and angular dimensions and raw Fourier components in each group was examined for evidence of bimodality of distribution. In the groups where sexes were known the mean, standard error of the mean and variance of each variable were calculated for each sex. The significance of the differences between means and variances was noted.

The second part of the univariate study was directed to an examination of the relationship between "size" (see chapter 2) and individual variables as expressed by the correlation coefficient.

Such a relationship is commonly modelled using the allometry equation $y = bx^a$ (where x = size variable, y = dependent variable and b and a describe the allometric relationship), the data being logged in order to allow the estimation of a and b by linear regression. Recently Albrecht and Gelvin (1987) have questioned the validity of this simple model in certain circumstances. In practice, however, it is both widely used and considered generally adequate for studies of comparative scaling (Gould, 1966, Jungers, pers. comm.). For this reason logged data were used in the calculation of correlation coefficients

between each variable and the size variables.

Inspection of bivariate plots of logged data vs. logged size variables failed to suggest any case in which males and females differed in their size relationship.

The following correlations were calculated within each sex of *Pan*, *Gorilla*, *Pongo*, and the caucasoid subgroup of *Homo* (the only racial group listed in table 2.1 in which sexual attribution is known):

a) between each of the first 40 logged Fourier components and the logged square root of the area of the midline projection (size variable); and

b) between each logged linear dimension and the logged square root of the area of the midline projection.

In those variables which have a significant correlation ($P<0.05$) with the size variable in both sexes linear models were used to compare the patterns of allometry between sexes (Freund and Littell, 1981). In no case was there significant ($P<0.05$, SAS, 1982, GLM) evidence of a sexual dimorphism in allometric patterns. This being the case sexes were pooled and further correlation coefficients between each logged variable and the logged size variable were calculated in each of *Pan*, *Pongo*, *Gorilla*, and the racial groups of mankind (see table 2.1 for a description of the samples).

The mean, range and variability of the square root of the midline area in the modern human groups were calculated in order to determine if the races of man differed in their patterns of size variation.

*Multivariate studies*

*Principal components analyses*

One approach to the study of within-group variation is to undertake a PCA of the covariance matrix of logged variables after Jolicoeur (1963a,b). Such analyses are explicit attempts to model the multivariate pattern of allometry within a group; if the first PC accounts for the majority of the total within-group variance and if the loadings (direction cosines) for each variable are of the same sign on this axis then PCI can be interpreted as a vector of relative scaling (Shea, 1985). The geometric mean of all variables is implicitly chosen as the size variable in the analysis. If all the loadings are of the same value and correspond to $p^{-1/2}$ (where p = the number of variables) the state of multivariate isometry exists. Loadings greater than this value indicate positive allometry and those which are smaller indicate negative allometry.

A preliminary attempt was made to utilise this approach in the study of the patterns of variability in the groups employed in this study. It revealed that, within several of the groups, especially the racial groups of mankind, the direction cosines for variables along the first PC were of different sign. This indicated that the first PC was not a pure vector of relative scaling.

For this reason an alternative approach was adopted. The principal components analyses described below use correlation matrices of variables because this gives equal weighting to the variability in each variable irrespective of its absolute magnitude (although in preliminary trials there was little difference in the outcomes of analyses using the covariance matrix and those using the

correlation matrix). The influence of size on the scores of crania on each PC was assessed by calculating the correlation coefficient between individual scores and the square root of the midline area of each cranium.

*Description of PCAs*

*Raw data*

The multivariate pattern of variation within each group of apes and each race of man was examined by principal components analysis of the correlation matrix of all 59 raw linear and angular dimensions and by PCA of the correlation matrix of the first 20 pairs of raw sine–cosine Fourier coefficients.

From each set of analyses ordinations of PC I vs. PC II were prepared for all groups and of PC I vs. PC II vs. PC III for those groups in which the sexes were known. The proportion of the total variance expressed by each principal component was noted and the correlation of the scores of individuals on each component with their size (area of mid–sagittal projection) was determined.

*Scaled data*

The scores of individuals on some components showed large correlations with their size. In order to discover whether these correlations related to a pure size increase or to a size increase plus shape change principal components analysis of (geometrically) scaled Fourier components and linear dimensions (angles were unaltered) was carried out. In order to allow a greater degree of comparability between analyses (linear and angular dimensions and Fourier data) only those 25

linear and angular measurements which were taken using midline landmarks were employed.

Similar sets of ordinations to those calculated from raw data were drawn and the proportion of variance accounted for by each component was recorded. The correlation between the scores of individuals on principal components and their sizes was calculated.

*Canonical analyses*

The final part of the multivariate study was directed to an examination of patterns of differences between sexes and groups.

Canonical analyses were undertaken using the 47 raw linear dimensions and the first 20 raw sine–cosine Fourier coefficient pairs from each of the male and female ape groups and the male and female caucasians (i.e. sexed groups).

An additional canonical analysis employed the variables listed in table 3.1. It was restricted to the two human groups of known sex (caucasoids and Hong Kong Chinese). An ordination of canonical axes I plus II plus III was prepared.

The SAS stepwise discriminant analysis program, STEPDISC, was used in order to determine those variables which best discriminated between sexes in the Hong Kong and caucasoid samples separately.

All statistical analyses were carried out using the "Leeds morphometric suite" and SAS (1982).

# RESULTS

## Univariate study

Table 3.2 lists those linear dimensions in which there is a significant difference between males and females. From this it can be seen that more cranial dimensions are sexually dimorphic in *Gorilla* and *Pongo* than in *Pan* and the caucasoids. In all cases where dimorphism is significant males are larger than females (except in *Pongo* where frontal height is smaller in males).

Table 3.3 lists differences in means between males and females in the raw Fourier data. Again, most dimorphisms are observed within *Gorilla* and *Pongo* with the values for Fourier components in males consistently larger than those in females.

These results conform with the naked eye observation that males are generally larger than females and that this size difference is relatively more pronounced within *Gorilla* and *Pongo* (see table 3.17). They indicate that there are some differences in the patterns of dimorphism between hominoids as is evidenced by the fact that there are some between-group differences in the variables which show significant dimorphism. Not all variables are proportionately different between sexes, suggesting that sexual dimorphism includes both size and shape differences.

It is of interest to enquire if the shape differences between the sexes are related to size differences. Table 3.4 lists for all groups (sexes pooled, see earlier) the significant ($p<0.05$) correlations between logged raw linear dimensions and the size variable (square root of midline area). Table 3.5 is

## TABLE 3.2

Means which are significantly different between sexes

O = P < 0.05 X = P < 0.01

| Variable | *Gor* | *Pon* | *Pan* | Cau |
|---|---|---|---|---|
| 1 Post orb. b. | X | X | | X |
| 2 bizygom. b. | X | X | X | X |
| 3 orbital breadth | X | X | | |
| 4 nasal breadth | X | X | X | |
| 5 infraorbit. b. | X | X | O | |
| 6 orbital ht. | X | X | | |
| 7 max. cran. b. | X | X | X | O |
| 8 palatal b. | X | X | | O |
| 9 foraminal b. | X | | | |
| 10 proj. len. mand. | X | X | X | X |
| 11 proj. ht. corond. | X | X | | |
| 12 proj. ht. ramus | X | X | | |
| 13 proj. ht. corpus | X | X | | O |
| 14 proj. l. corpus | X | X | X | O |
| 15 bicondylar b. | X | X | X | X |
| 16 coronial b. | X | X | O | O |
| 17 bigonial b. | X | X | X | O |
| 18 condylar len. | X | X | X | |
| 19 min. rameal b. | X | X | X | |
| 20 molar–prem. chd. | X | X | O | X |
| 21 bimental b. | X | X | O | O |
| 22 max. len. | X | X | X | X |
| 23 frontal chd. | X | X | | |
| 24 frontal ht. | | X* | | |
| 25 parietal chd. | X | | | |
| 26 parietal ht. | X | | | |
| 27 occipital chd. | X | X | | |
| 28 occipital ht. | | | | O |
| 29 foraminal len. | | | | |
| 30 auricular ht. | X | X | | X |
| 31 basibreg. ht. | X | X | | X |
| 32 basinasal len. | X | X | X | X |
| 33 basi–infraorb. l. | X | X | O | O |
| 34 basi–staph. len. | X | X | O | |
| 35 basi–prosth. len. | X | X | X | X |
| 36 basi–infrdent. l. | X | X | X | X |
| 37 basi–mental len. | X | X | X | X |
| 38 basi–mand. len. | X | X | | O |
| 39 basi–symph. len. | X | X | X | X |
| 40 basi–gon. len. | X | X | O | O |
| 41 palatal len. | X | X | X | O |
| 42 nasal ht. | X | X | X | X |
| 43 upp. face ht. | X | X | X | X |
| 44 tot. face ht. | X | X | X | X |
| 45 max–mandib. ht. | X | X | X | X |
| 46 subnasal ht. | | X | | |
| 47 symphyseal ht. | X | X | X | X |

In all cases variable means are larger in males than in females except*

## TABLE 3.3

Means which are significantly different between sexes

O = P<0.05  X = P<0.01

| Variable | *Gor.* | *Pon.* | *Pan.* | Cau. |
|---|---|---|---|---|
| Cosine 1 | | X | O | |
| Sine 1 | X | | X | O |
| Cosine 2 | X | X | X | |
| Sine 2 | X | X | O | O |
| Cosine 3 | X | X | | O |
| Sine 3 | X | | X | |
| Cosine 4 | X | X | | |
| Sine 4 | O | | | |
| Cosine 5 | X | O | X | |
| Sine 5 | X | | | |
| Cosine 6 | X | X | | |
| Sine 6 | | | | |
| Cosine 7 | | X | | |
| Sine 7 | O | | | |
| Cosine 8 | X | X | | |
| Sine 8 | | X | | O |
| Cosine 9 | X | X | | O |
| Sine 9 | X | X | | |
| Cosine 10 | X | X | | |
| Sine 10 | X | | | |
| Cosine 11 | O | X | | |
| Sine 11 | | X | | |
| Cosine 12 | X | X | | |
| Sine 12 | | | | |
| Cosine 13 | O | X | | |
| Sine 13 | X | | | |
| Cosine 14 | | X | | |
| Sine 14 | | O | | |
| Cosine 15 | X | X | | |
| Sine 15 | O | O | | |
| Cosine 16 | O | X | | |
| Sine 16 | | O | | X |
| Cosine 17 | O | | | |
| Sine 17 | | X | | |
| Cosine 18 | X | O | | |
| Sine 18 | | X | | |
| Cosine 19 | | O | | |
| Sine 19 | X | X | | |
| Cosine 20 | X | X | | |
| Sine 20 | O | X | | |

## TABLE 3.4

Correlations between each logged variable and the logged square root of the midline area within groups. Sexes are pooled.

All significant correlations ($P<0.05$) are listed (* indicates $P<0.01$)

| Variable | Ger. | Pon. | Pan. | Aus. | Cau. | Mon. | Neg. |
|---|---|---|---|---|---|---|---|
| N= | 61 | 54 | 60 | 34 | 30 | 30 | 30 |
| postorb. b. | .61 * | .55 * | .41 * | .56 * | .39 | .41 | .59 * |
| bizygom. b. | .90 * | .92 * | .68 * | .69 * | .50 * | .51 * | .61 * |
| orbital. b. | .70 * | .74 * | .53 * | .50 * | | | .58 * |
| nasal. b. | .67 * | .71 * | .57 * | .33 | | | |
| infraorb. b. | .76 * | .80 * | .63 * | .48 * | | .43 | .57 * |
| orbital. ht. | .42 * | .49 * | .36 * | .42 | | .37 | |
| max. cran. b. | .67 * | .85 * | .69 * | .47 * | .53 * | | |
| palatal b. | .47 * | .52 * | .29 | .44 * | .43 | | .56 * |
| foraminal b. | .33 * | | | .47 * | | .53 * | |
| proj. l. mand. | .90 * | .89 * | .63 * | .73 * | .39 | .34 | .49 * |
| proj. ht. coro. | .84 * | .89 * | .48 * | .55 * | | .40 | .64 * |
| proj. ht. ram. | .67 * | .82 * | .36 * | .36 | | | .61 * |
| proj. ht. corp. | .66 * | .83 * | | .45 * | | | .58 * |
| proj. l. corp. | .84 * | .86 * | .65 * | .66 * | | | .68 * |
| bicondyl. b. | .83 * | .86 * | .55 * | .50 * | .44 | .45 | .50 * |
| coronal b. | .76 * | .80 * | .54 * | .57 * | | .41 | .52 * |
| bigonial b. | .79 * | .84 * | .44 * | .63 * | .44 | .42 | .37 |
| condyle l. | .75 * | .88 * | .40 * | .45 * | .37 | | |
| min. ram. b. | .89 * | .89 * | .60 * | .58 * | | .37 | .60 * |
| mol.-prem. chd. | .45 * | .41 * | .32 | .36 | .38 | | |
| bimental b. | .70 * | .82 * | .47 * | .46 * | .36 | | |
| max. len. | .92 * | .91 * | .84 * | .92 * | .84 * | .84 * | .89 * |
| frontal chd. | .78 * | .64 * | .55 * | .62 * | .62 * | .80 * | .77 * |
| frontal ht. | | | | | | .46 * | .47 * |
| parietal chd. | .41 * | | .42 * | .67 * | .50 * | .73 * | .59 * |
| parietal ht. | -.26 | | .28 | | | | |
| occ. chd. | .60 * | .57 * | | .52 * | .54 * | .75 * | .58 * |
| occ. ht. | | | | .45 * | .55 * | .72 * | .44 |
| foraminal l. | | .31 | | .56 * | | .40 | |
| auricular ht. | .56 * | .78 * | .37 * | .84 * | .84 * | .84 * | .77 * |
| basibreg. ht. | .77 * | .86 * | .58 * | .77 * | .84 * | .82 * | .80 * |
| basinasal l. | .94 * | .89 * | .70 * | .74 * | .51 * | .68 * | .71 * |
| basi-infraorb. l. | .95 * | .91 * | .60 * | .41 | .45 | .44 | .79 * |
| basi-staph. l. | .89 * | .88 * | .34 * | | | | .71 * |
| basi-pros. l. | .95 * | .92 * | .59 * | .49 * | .36 | | .75 * |
| basi-infrdnt. l. | .93 * | .91 * | .61 * | .63 * | .61 * | | .70 * |
| basi-mental l. | .90 * | .90 * | .47 * | .54 * | .52 * | | .62 * |
| basi-mand. l. | .79 * | .84 * | .31 | | | | |
| basi-symph. l. | .91 * | .90 * | .49 * | .56 * | .45 | | .72 * |
| basi-gon. l. | .68 * | .82 * | | | | | |
| palate l. | .91 * | .86 * | .60 * | .47 * | .42 | .39 | .68 * |
| nasal ht. | .86 * | .85 * | .48 * | .67 * | .40 | .52 * | .49 * |
| upp. face. ht. | .83 * | .86 * | .49 * | .77 * | | .61 * | .74 * |
| tot. face. ht. | .86 * | .88 * | .60 * | .78 * | .50 * | .65 * | .69 * |
| max-mandib. ht. | .80 * | .84 * | .46 * | .75 * | .52 * | .46 * | .46 * |
| subnasal ht. | | .56 * | | .60 * | | | .55 * |
| symphyseal ht. | .80 * | .83 * | .55 * | .63 * | .38 | .39 | |

## TABLE 35

Correlations between each logged variable and the logged square root of the midline area within groups. Sexes are pooled.

All significant correlations ($P<0.05$) are listed (* indicates $P<0.01$)

| Variable | | Gor. | Pon. | Pan. | Aus. | Cau. | Mon. | Neg. |
|---|---|---|---|---|---|---|---|---|
| N= | | 61 | 54 | 60 | 34 | 30 | 30 | 30 |
| Cosine | 1 | | -.74 * | | -.48 * | | | -.58 * |
| Sine | 1 | .58 * | | .30 | | | | .61 * |
| Cosine | 2 | .87 * | .85 * | .40 * | | | | |
| Sine | 2 | -.35 * | -.38 * | | .35 | | .49 * | .58 * |
| Cosine | 3 | -.46 * | .46 * | | .34 | | | .62 * |
| Sine | 3 | -.75 * | | | .60 * | | | |
| Cosine | 4 | .63 * | .57 * | | | | | |
| Sine | 4 | -.26 | | | .42 | | | |
| Cosine | 5 | .48 * | .38 * | | | | | .44 |
| Sine | 5 | | | | .52 * | | .45 | .42 |
| Cosine | 6 | .72 * | .60 * | | .54 * | | .54 * | .64 * |
| Sine | 6 | | | | .53 * | .36 | .37 | |
| Cosine | 7 | | .50 * | | .35 | | | .56 * |
| Sine | 7 | .39 * | | | | | | |
| Cosine | 8 | .33 * | .46 * | | | | | |
| Sine | 8 | | .46 * | | | | | |
| Cosine | 9 | .66 * | .58 * | | | | | |
| Sine | 9 | -.46 * | .45 * | | | | | |
| Cosine | 10 | .64 * | .58 * | .26 | | | .41 | |
| Sine | 10 | -.30 | | | | .39 | | |
| Cosine | 11 | .34 * | .62 * | | | | | |
| Sine | 11 | | .43 * | | | | | |
| Cosine | 12 | .33 * | .73 * | | -.38 | | | |
| Sine | 12 | | | | | | | .44 |
| Cosine | 13 | -.32 | .54 * | | | | | |
| Sine | 13 | -.50 * | | | | | | |
| Cosine | 14 | | .48 * | | | | | |
| Sine | 14 | | .32 | | | | | |
| Cosine | 15 | .47 * | .37 * | | | | | |
| Sine | 15 | -.25 | .37 * | | | | | .40 |
| Cosine | 16 | .34 * | .38 * | | | | | |
| Sine | 16 | | .34 | | | | | .38 |
| Cosine | 17 | .30 | .30 | | | | | |
| Sine | 17 | | .41 * | | | | | |
| Cosine | 18 | .47 * | .31 | | | | | |
| Sine | 18 | | .41 * | | | | | |
| Cosine | 19 | | .31 | | | | | |
| Sine | 19 | -.40 * | .46 * | | | | | |
| Cosine | 20 | .61 * | .35 * | | | | | |
| Sine | 20 | | .42 * | | .39 | | | |

similar but relates to correlations between the logged Fourier components and the size variable.

Comparison of table 3.4 with table 3.2 and of table 3.5 with table 3.3 indicates that, for both the Fourier components and linear dimensions, those groups which show a large number of significant dimorphisms in variable magnitude also have a large number of significant correlations between the size and other variables. Furthermore, in general, those variables which show a significant sexual difference are also significantly correlated with the size variable. There remains, however, a component of sexual dimorphism which does not appear to be entirely explained by a relationship to the size variable employed in these studies. For example the projected height of the mandibular corpus shows a significant dimorphism in caucasoids whilst it has no significant correlation with the chosen size variable in this group. This may well be the result of an inadequate choice of size variable or of inadequate sample size to show significance. Alternatively it may be a finding which would be borne out by more extensive data and a different choice of size variable.

A further finding from the results of tables 3.4 and 3.5 is that there are marked differences between the racial groups of *Homo* in the number of significant correlations with the size variable, in the patterns of variables which show a significant correlation with the size variable and in the magnitudes of the correlations of certain variables with the size variable (e.g. bigonial breadth, basi–infraorbital length, cosine 7 though none of these differences reaches statistical significance of $P<0.05$). These differences may simply be the result of racial differences in cranial size and cranial size variability although the results of table 3.6 indicate that such differences do not exist in these groups.

Table 3.6 lists the mean value of the square root of the midline area in the races of man together with information relating to the range and variability of this measure of size. The mean and the range of the size variable are nearly the same in all races. It should also be noted that none of the coefficients of variation show a significant difference (at the 2% level) between races.

TABLE 3.6

Cranial size differences between the races of man

Size variable = sqrt. midline area (cm)

| RACE | MEAN | MIN. | MAX. | C.V. x 100 |
|---|---|---|---|---|
| Australoid | 14.2 | 13.1 | 15.3 | 4.14 |
| Caucasoid | 14.5 | 13.6 | 15.4 | 3.24 |
| Mongoloid | 14.2 | 13.1 | 15.3 | 4.09 |
| Negroid | 14.4 | 13.3 | 15.5 | 3.70 |

C.V. = coefficient of variation

Table 3.7 lists those raw linear dimensions in each group in which there is a significant difference in variance between males and females. Table 3.8 lists significant sexual differences in variances in the raw Fourier components.

These tables agree in indicating that different patterns of dimorphism of variances characterise different groups. Further concordance lies in the common

## TABLE 3.7

**Variances which are significantly different between sexes**

O = P < 0.05 X = P < 0.01

| Variable | | *Gor* | *Pon* | *Pan* | Cau |
|---|---|---|---|---|---|
| 1 | post orb. b. | | X | | |
| 2 | bizygom. b. | O | | O | |
| 3 | orbital breadth | | | | |
| 4 | nasal breadth | | | | |
| 5 | infraorbit. b. | X | | | |
| 6 | orbital ht. | | | | |
| 7 | max. cran. b. | X | | | O |
| 8 | palatal b. | | | | |
| 9 | foraminal b. | | | | |
| 10 | proj. len. mand. | | O | | |
| 11 | proj. ht. corond. | | X | | |
| 12 | proj. ht. ramus. | O | | | |
| 13 | proj. ht. corpus. | | O | | |
| 14 | proj. l. corpus. | O | | | |
| 15 | bicondylar b. | O | | O | |
| 16 | coronial b. | O | | | |
| 17 | bigonial b. | | | | |
| 18 | condylar len. | | | | |
| 19 | min. rameal b. | | | | |
| 20 | molar–prem. chd. | X | | | |
| 21 | bimental b. | | X | | O |
| 22 | max. len. | | | | |
| 23 | frontal chd. | X | | | |
| 24 | frontal ht. | | | | |
| 25 | parietal chd. | O | | | |
| 26 | parietal ht. | | | | |
| 27 | occipital chd. | | | | |
| 28 | occipital ht. | | | | |
| 29 | foraminal len. | | | | |
| 30 | auricular ht. | | | | |
| 31 | basibreg. ht. | | | | |
| 32 | basinasal len. | X | | | X |
| 33 | basi–infraorb. l. | X | | | O |
| 34 | basi–staph. len. | | | | O |
| 35 | basi–prosth. len. | X | | | |
| 36 | basi–infrdent. l. | | | | |
| 37 | basi–mental len. | | | O | |
| 38 | basi–mand. len. | X | | O | |
| 39 | basi–symph. len. | O | | O | |
| 40 | basi–gon. len. | | O | O | |
| 41 | palatal len. | | | O | |
| 42 | nasal ht. | X | X | O | O |
| 43 | upp. face ht. | X | X | | |
| 44 | tot. face ht. | | X | X | |
| 45 | max–mandib. ht. | | X | O | |
| 46 | subnasal ht. | | O | | |
| 47 | symphyseal ht. | O | | | |

## TABLE 3.8

Variances which are significantly different between sexes

O = P<0.05 X = P<0.01

| Variable | | *Gor.* | *Pon.* | *Pan.* | Cau |
|---|---|---|---|---|---|
| Cosine | 1 | O | | | |
| Sine | 1 | X | X | O | |
| Cosine | 2 | | O | | |
| Sine | 2 | X | O | O | |
| Cosine | 3 | O | | | |
| Sine | 3 | | | | |
| Cosine | 4 | X | | | |
| Sine | 4 | | | | |
| Cosine | 5 | O | | O | |
| Sine | 5 | O | | | O |
| Cosine | 6 | | | | |
| Sine | 6 | X | | | |
| Cosine | 7 | X | | | |
| Sine | 7 | | | | |
| Cosine | 8 | | | | |
| Sine | 8 | O | O | | |
| Cosine | 9 | | | X | |
| Sine | 9 | | | | |
| Cosine | 10 | | | | |
| Sine | 10 | | | | |
| Cosine | 11 | | | X | |
| Sine | 11 | | | | |
| Cosine | 12 | X | | | |
| Sine | 12 | | | | O |
| Cosine | 13 | | | | |
| Sine | 13 | | | | X |
| Cosine | 14 | | | | |
| Sine | 14 | | | | |
| Cosine | 15 | | | | |
| Sine | 15 | | | | |
| Cosine | 16 | | | O | |
| Sine | 16 | | | | |
| Cosine | 17 | | | | |
| Sine | 17 | | | | |
| Cosine | 18 | | | | |
| Sine | 18 | | | | |
| Cosine | 19 | O | | O | |
| Sine | 19 | | | | |
| Cosine | 20 | | | O | |
| Sine | 20 | O | | | |

finding of a consistently greater variance in males than in females where a significant dimorphism exists and in the finding that dimorphism in variances of linear dimensions is most pronounced in *Gorilla* and least in caucasoids.

In this study the Fourier components show a pattern of dimorphism of variance consistent with that found by Oxnard (1987) in a study of dental dimensions. He noted that in the chimpanzee and gorilla there was a higher number of dimorphisms in variance than in other hominoids. The findings from linear dimensions (table 3.7), however, contrast in showing a similar number of dimorphisms of variance in *Pongo* and *Pan*.

There is a relationship between a dimorphism in variances and a marked correlation with the size variable (see tables 3.4, 3.5, 3.7 and 3.8). It appears, however, to be far less pronounced than that between a dimorphism in variable magnitude and a marked correlation with the size variable. Thus, in the case of the linear dimensions there are many variables which show a marked correlation with the size variable but few of these have a significant sexual dimorphism of variances. In the case of the Fourier data a substantial proportion of components show a significant sexual difference in variances in the absence of a significant correlation with the size variable.

Summary of the Univariate findings

Within each group variables differ in their degree of dimorphism. This implies that sexual dimorphism involves a shape dimorphism. There is some variation in the pattern of sexual shape dimorphism between the genera and the

races of mankind reflected in the differences in the variables which show sexual differences in means in different groups.

In addition to a sexual shape dimorphism there appears to be a sexual dimorphism of variances in some variables. The variables which show this dimorphism of variances are not constant between groups. This implies a degree of between-group variability also exists in this phenomenon.

The univariate studies demonstrate that those variables which differ in magnitude between sexes are, in general, those which have a marked correlation with size. It seems that, to a large extent, size and sexual shape differences are related in these groups.

By contrast there is a less clear association between sexual differences in variances and a marked correlation with the size variable.

## Multivariate study

The Multivariate study examined both within and between-group variability.

### Patterns of within-group variability

Patterns of within-group variability were examined by principal component analysis.

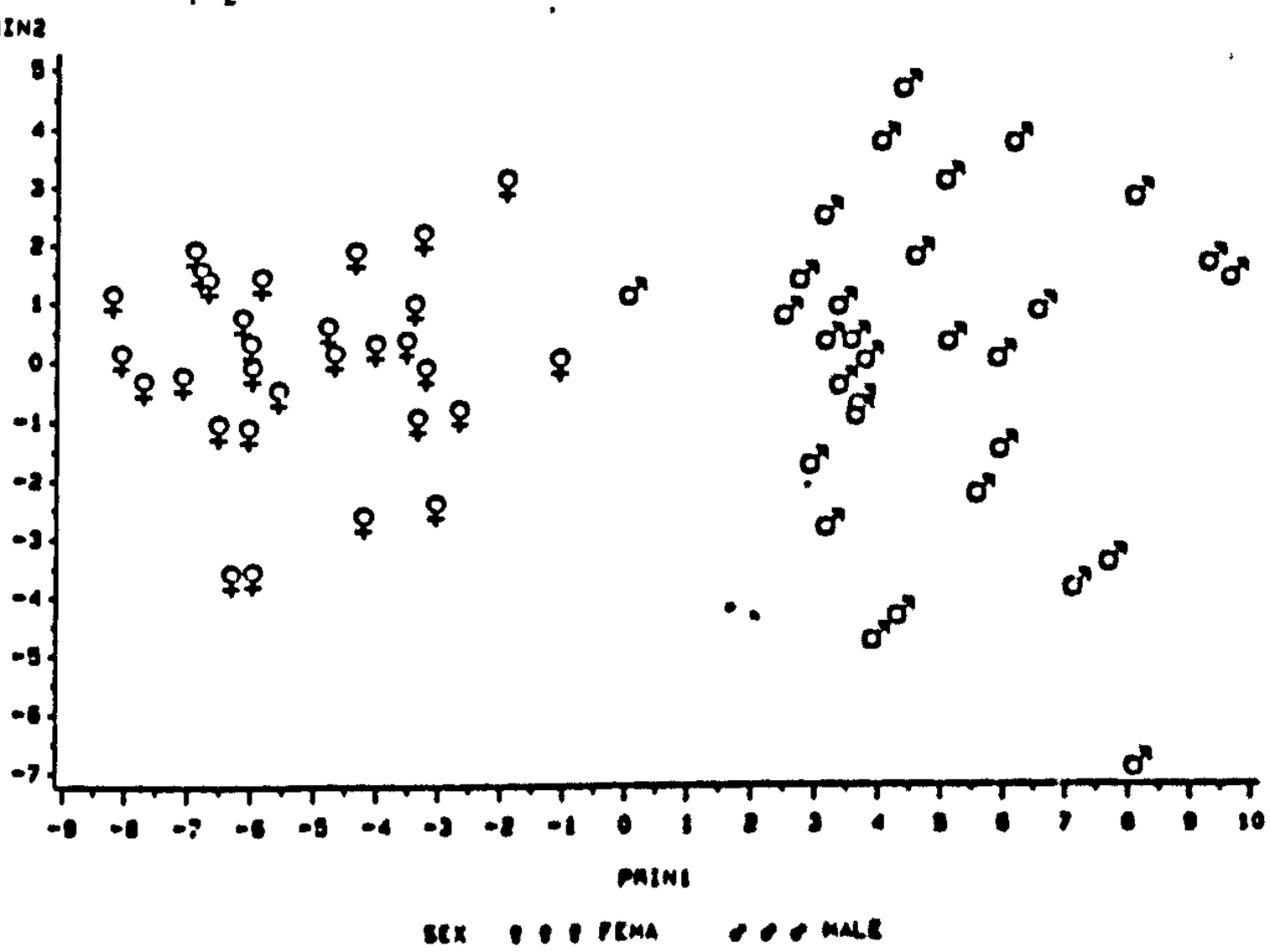
### I. Raw data

*PCAs of 59 linear and angular measurements*

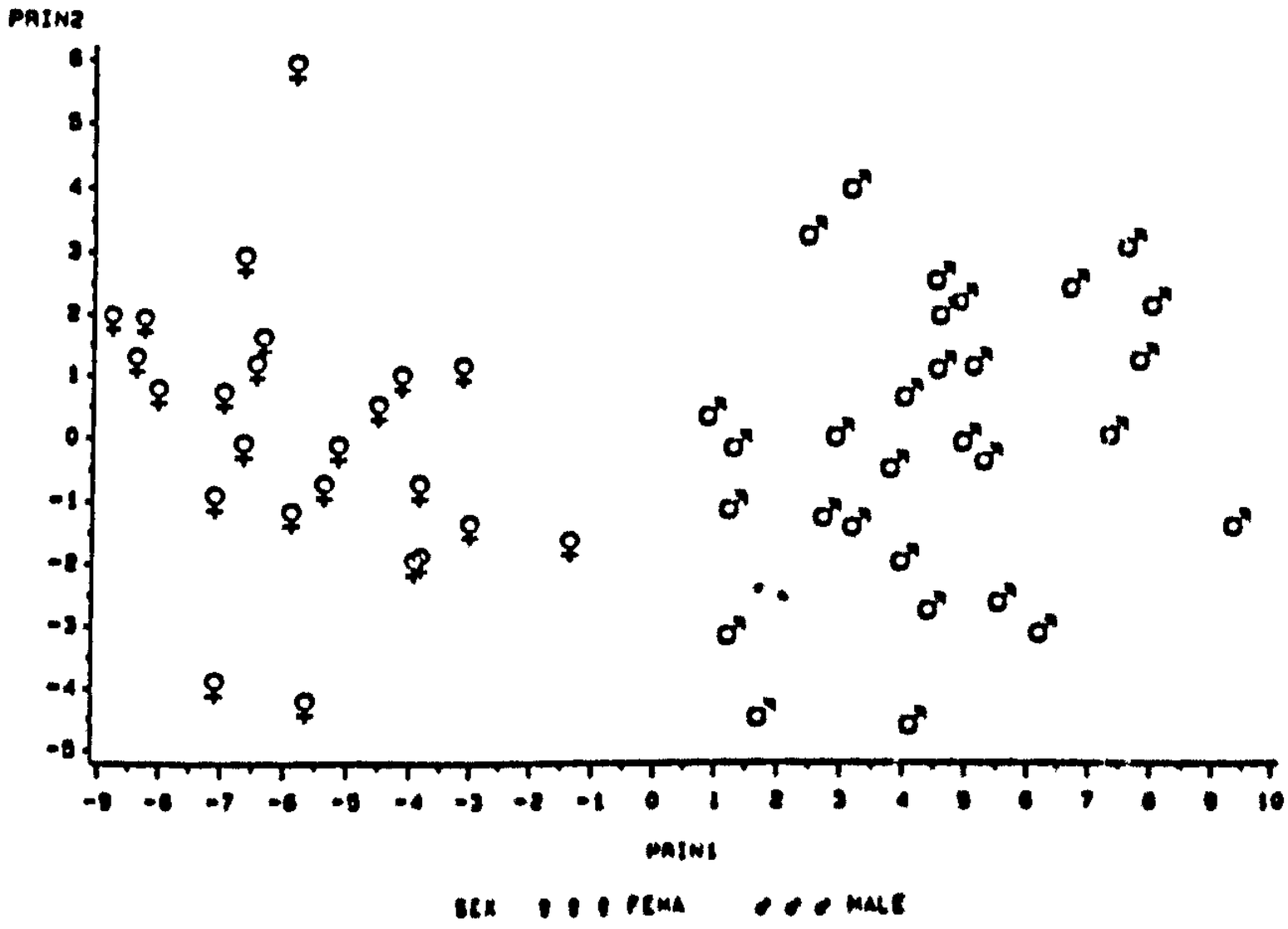
Plots of the scores of the *Gorilla* and *Pongo* samples on principal components (PCs) I and II are given in figure 3.1 and on PCs I and II and III in figure 3.2. Reference to table 3.9 shows that about 65% of the total within-group variance is represented by the first three components. Figure 3.1 clearly demonstrates a separation between males and females in both groups. Neither PC II nor PC III contribute to this separation (figs 3.1 and 3.2). In both groups PC I accounts for 50% of the total within-group variance which appears to be variance associated with sexual dimorphism.

The influence of size upon sexual dimorphism in these groups is illustrated by the fact that (from table 3.10) the score of individuals on principal component I correlates 0.99 with the square root of the mid-line area of each. The univariate finding of greater variability within males is not evident from the

FIGURE 3.1 – Principal Components Analysis of 59 raw linear and angular dimensions



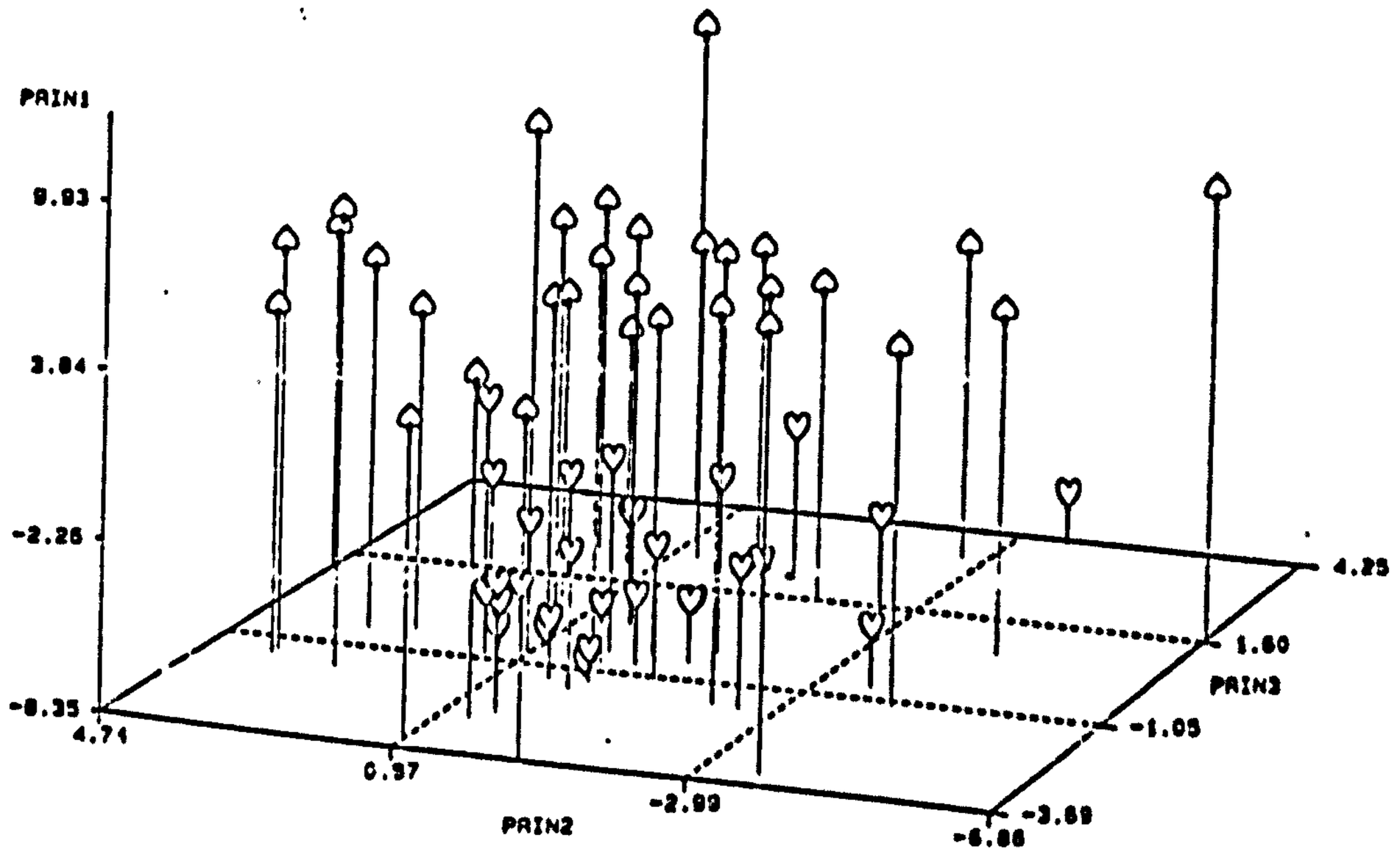

a. *Gorilla*



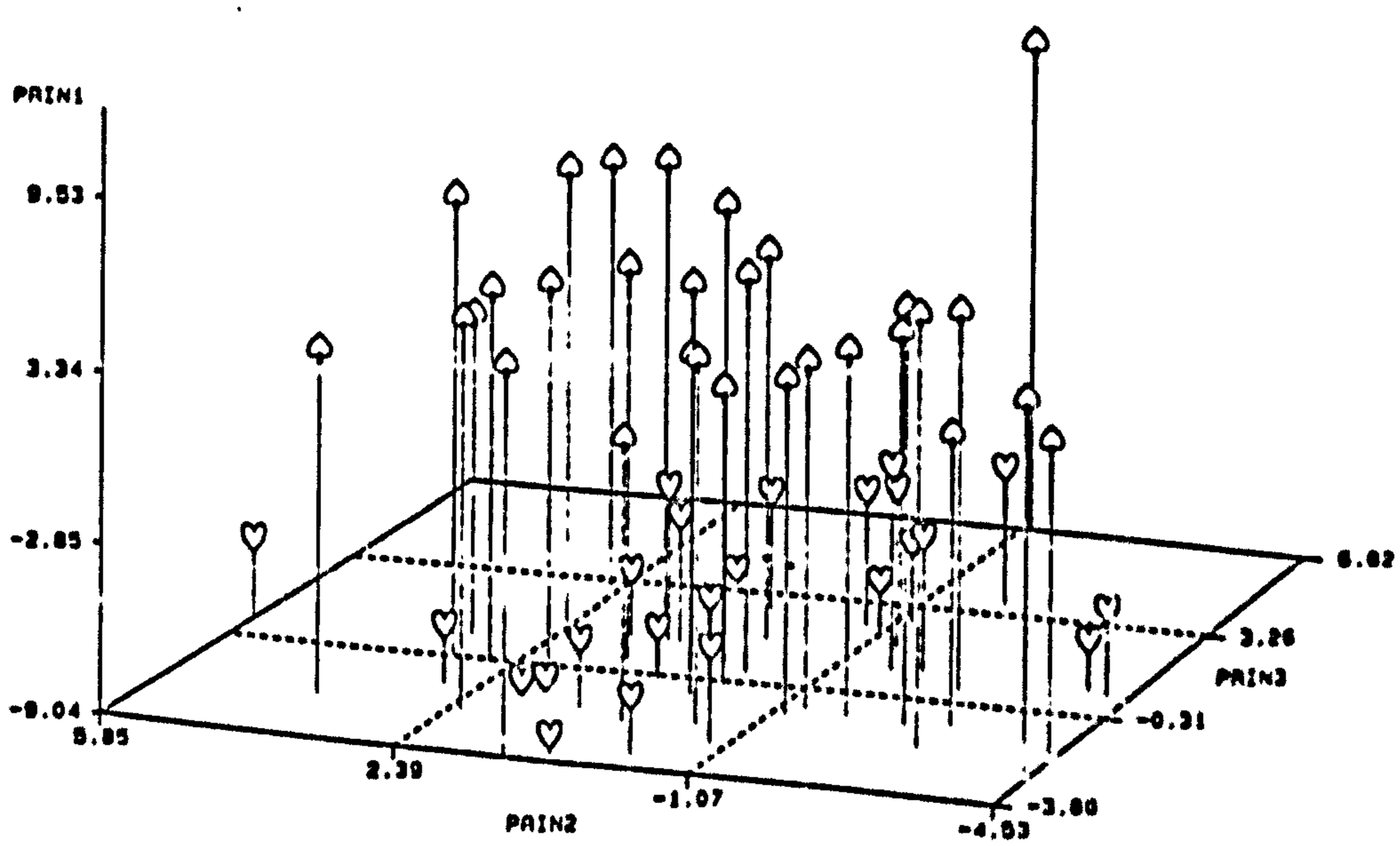

b. *Pongo*

Fig 3.1

FIGURE 3.2 – Principal Components Analysis of 59 raw linear angular dimensions




a. *Gorilla*




b. *Pongo*

Key: hearts = females, spades = males

Fig 3.2

## TABLE 3.9

**Principal Components Analysis of 59 raw linear and angular dimensions**

**Proportion (%) of total variance accounted for by the first n principal components (cumulative)**

| n = 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| group | | | | |
| *Gorilla* | 50 | 58 | 63 | 68 | 72 |
| *Pongo* | 51 | 59 | 66 | 71 | 75 |
| *Pan* | 29 | 41 | 50 | 57 | 62 |
| *Homo* : | | | | | |
| Cauc. | 24 | 38 | 48 | 56 | 63 |
| Mon. | 27 | 42 | 51 | 59 | 67 |
| Neg. | 30 | 42 | 51 | 59 | 64 |
| Aust. | 35 | 47 | 54 | 61 | 66 |

## TABLE 3.10

**Principal Components Analysis of 59 raw linear and angular dimensions**

**The correlation of the size variable (square root of area of midline tracing) with the scores of individuals on PC no:**

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| *Gorilla* | 0.99** | 0.03 | 0.02 | 0.02 | 0.02 |
| *Pongo* | 0.99** | 0.02 | −0.02 | 0.00 | 0.03 |
| *Pan* | 0.99** | 0.04 | 0.05 | 0.10 | 0.03 |
| *Homo:* | | | | | |
| Cauc. | 0.98** | 0.02 | 0.10 | 0.03 | 0.02 |
| Mon. | 0.99** | 0.06 | 0.05 | 0.00 | 0.10 |
| Neg. | 0.99** | −0.01 | 0.00 | 0.03 | 0.01 |
| Aust. | 0.99** | 0.00 | 0.02 | 0.04 | 0.00 |

**P < 0.01 = ****

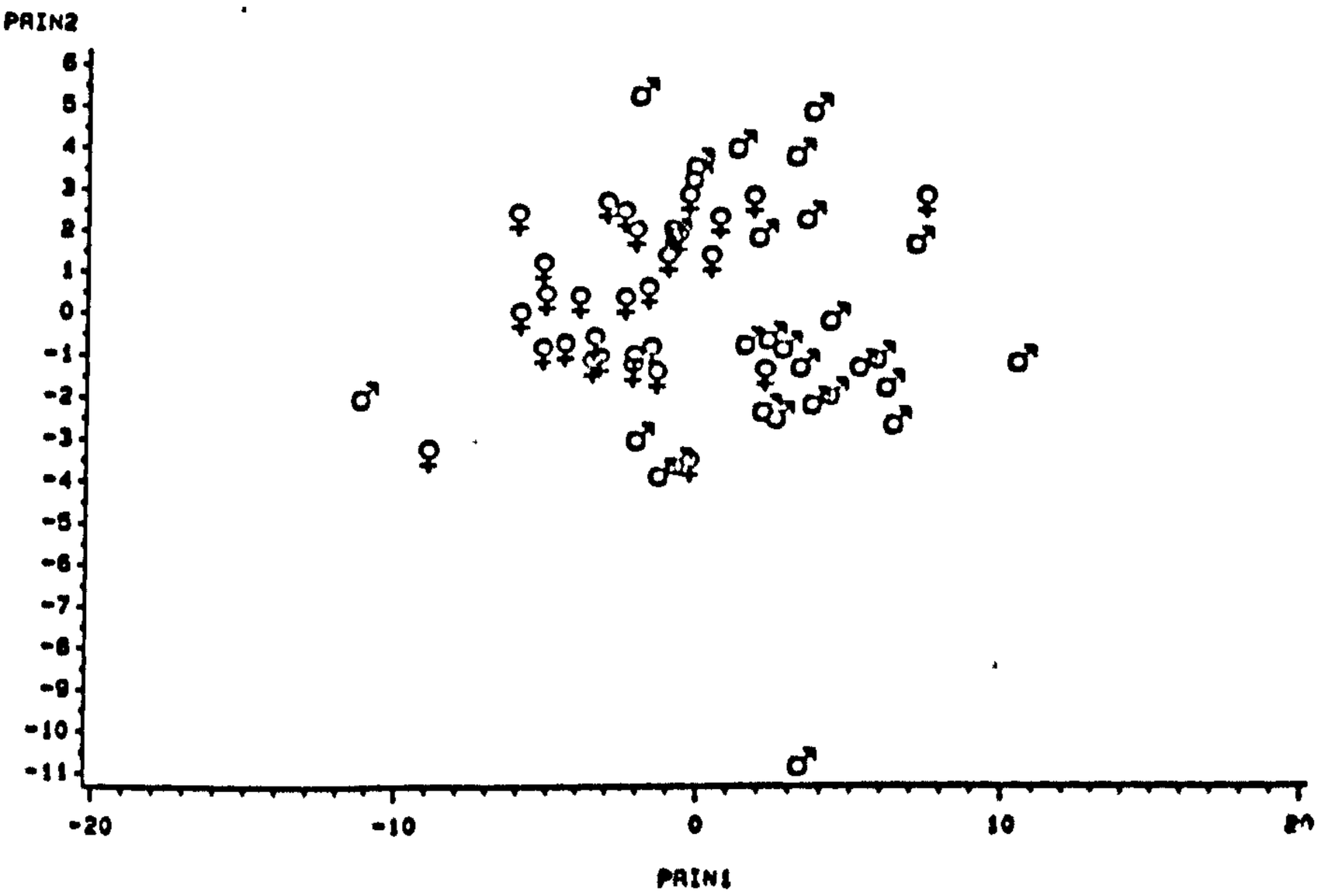
PCAs of *Pongo* and only marginally so in the case of *Gorilla*.

It is interesting to compare the pattern of variability revealed by PCA of the *Pan* sample with those described above. Figures 3.3 and 3.4a are plots of PC's I and II and PC's I and II and III respectively. The sexes are not clearly separated and the first three components account for only 50% (table 3.9) of the total within-group variability. Despite the high correlation of size with first PC (table 3.10: 0.99) this accounts for only 29% of the total within-group variability. Size makes a far smaller (about half of that in *Gorilla* and *Pongo*) contribution to within-group variability and this is reflected in a less clear pattern of sexual dimorphism. Related to this is the fact that more (5) PCs are required to account for a similar proportion of within-group variability as the first 3 PCs in the analyses of *Gorilla* and *Pongo* (see table 3.9). Other sources of variability (i.e. not size related) are proportionately more important. The chimpanzees form more of a hypersphere than a hyperellipse.

Plots of PCs I and II and of PCs I and II and III for the caucasoids are drawn in figures 3.5a and 3.4b respectively. In this human sample sexes were known from records. PC I shows a much clearer sexual separation than was apparent within the chimpanzees. This is despite the fact that it accounts for a smaller proportion of the total within-group variability (24% as opposed to 29% in *Pan* – table 3.9). Scores of individuals on PC I correlate 0.98 with their square root of the mid-line projection (table 3.10).

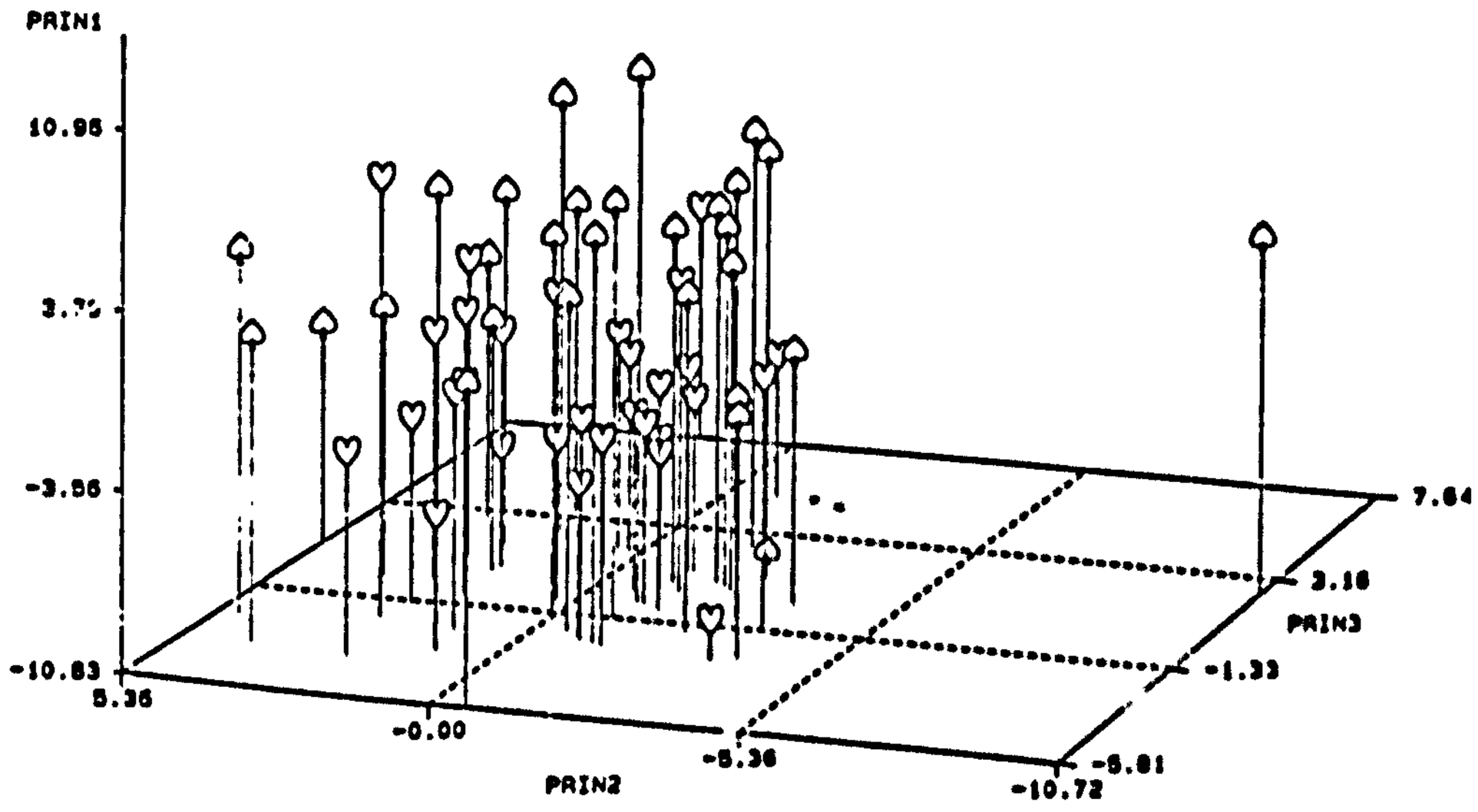
From table 3.17 it can be seen that the absolute "size" difference between the sexes of *Pan* is 0.32cm and between the sexes of caucasoids (the only human group of known sex) it is 0.6cm. The relative size difference (male size/female size) is 1.03 in *Pan* and 1.04 in caucasoids. From both measures of sexual

FIGURE 3.3 – Principal Components Analysis of 59 raw linear and angular dimensions

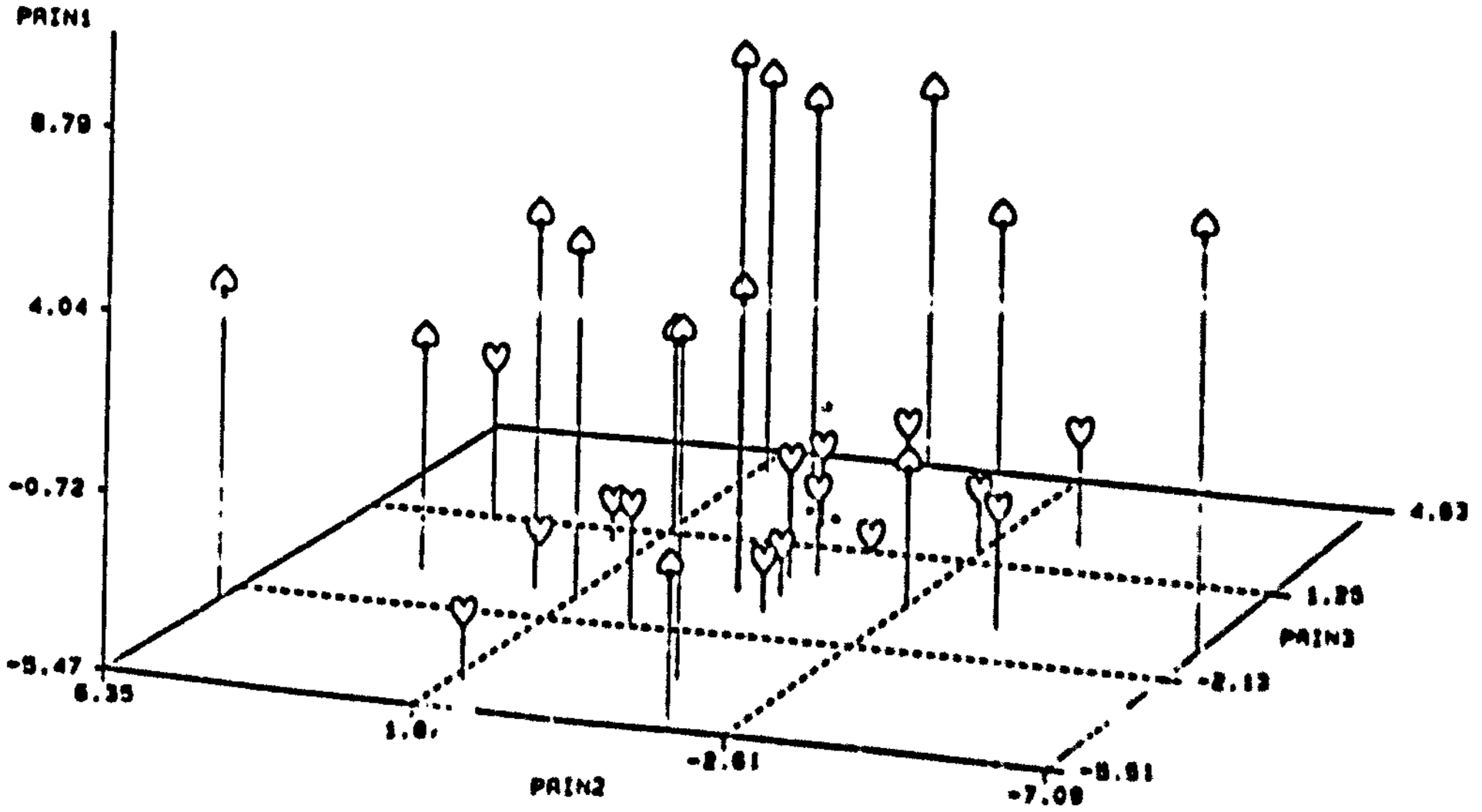



*Pan*

FIGURE 3.4 – Principal Components Analysis of 59 raw linear and angular dimenions




a. *Pan*

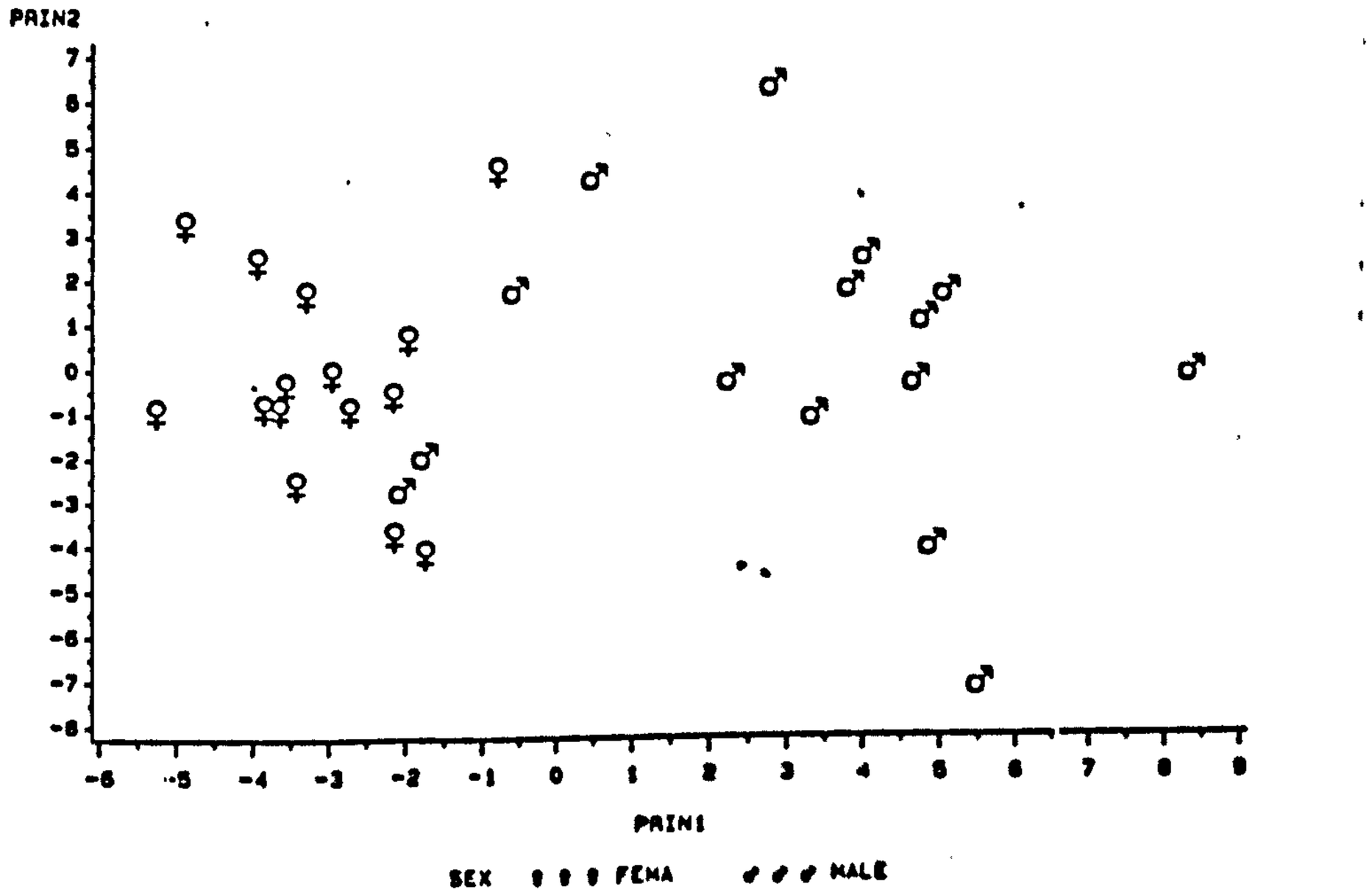



b. Caucasoid

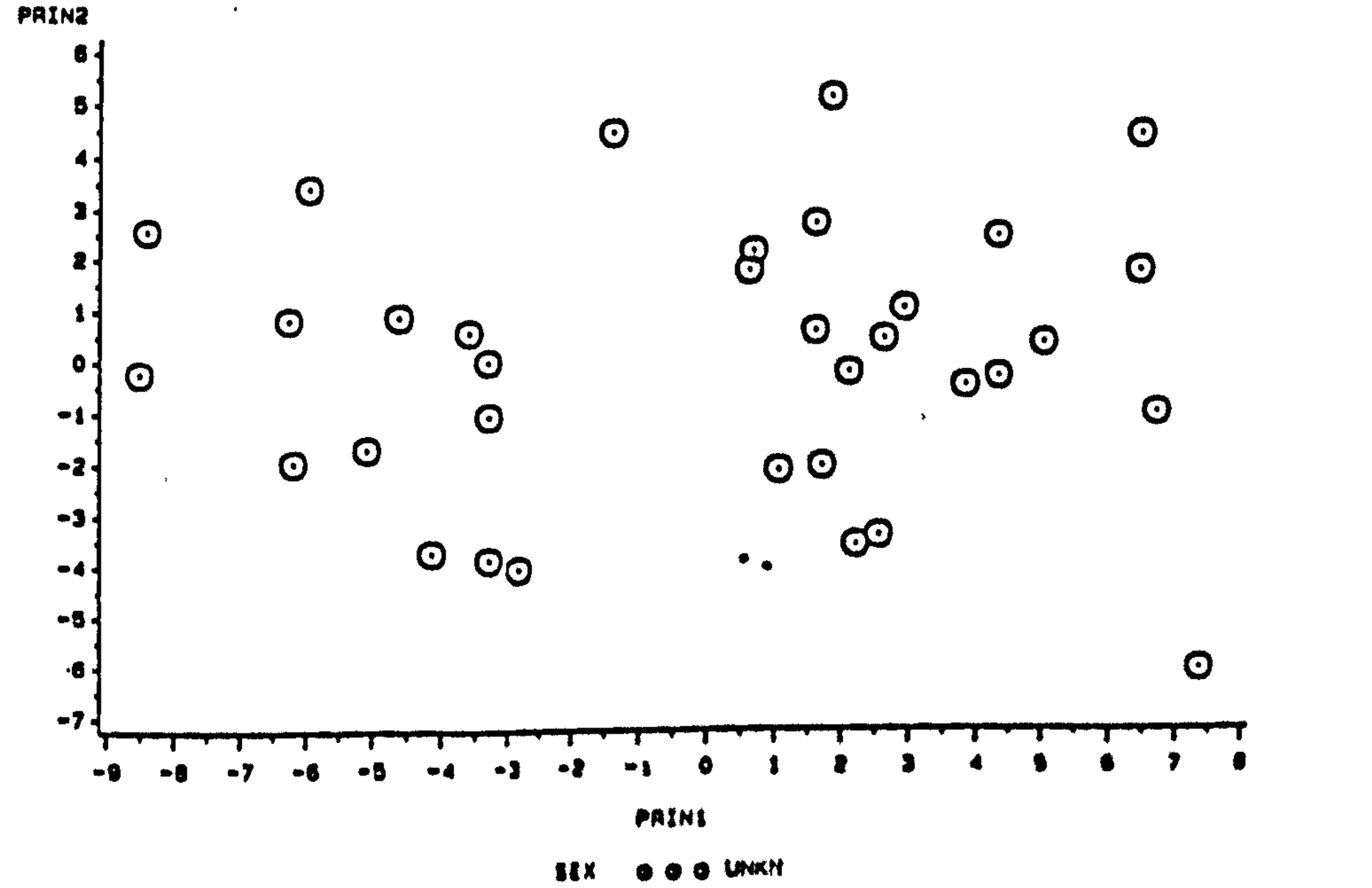
Key: hearts = females, spades = males

Fig 3.4

FIGURE 3.5 – Principal Components Analysis of 59 raw linear and angular dimensions




a. Caucasoids



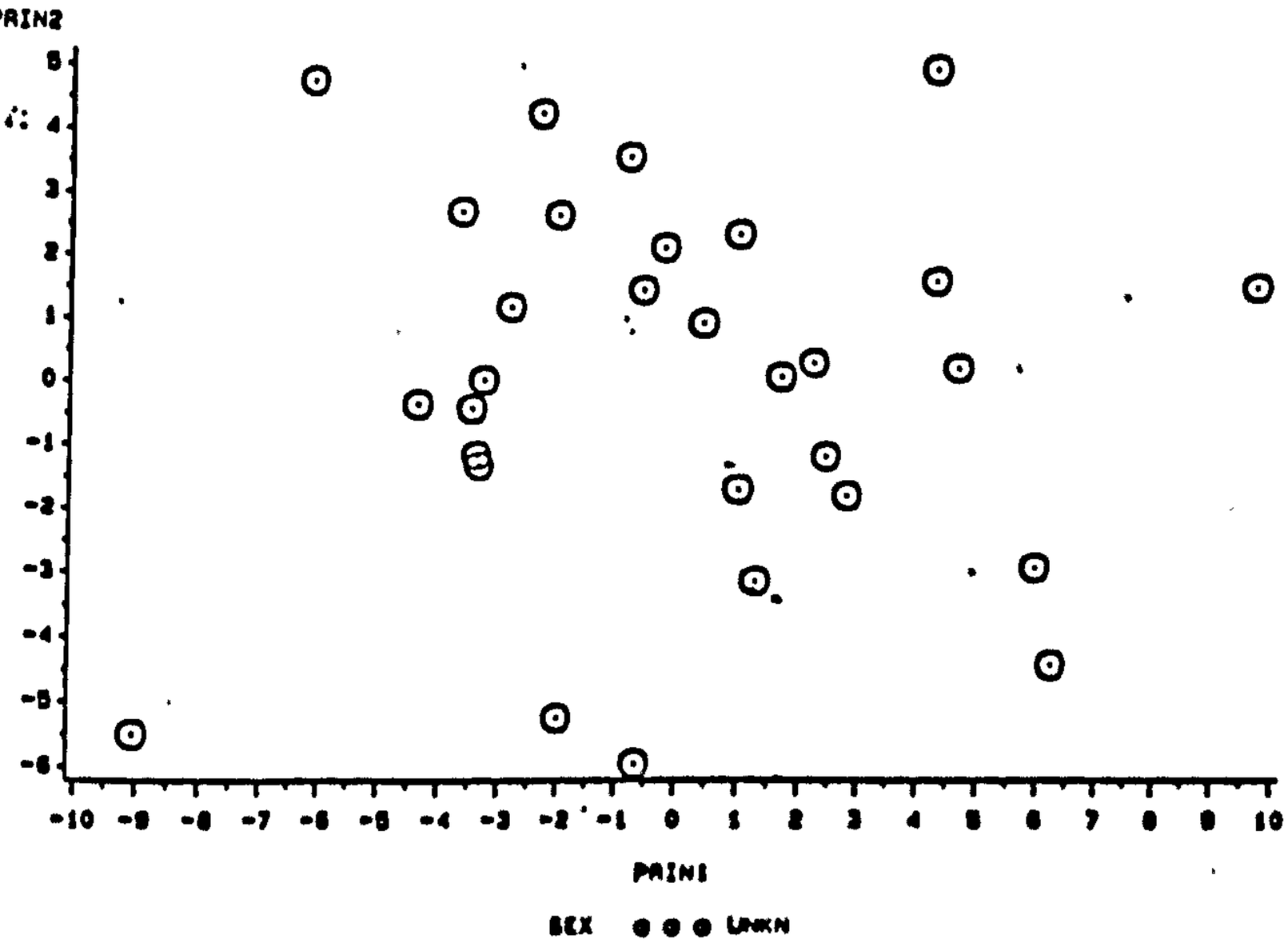

b. Australoids

Fig 3.5

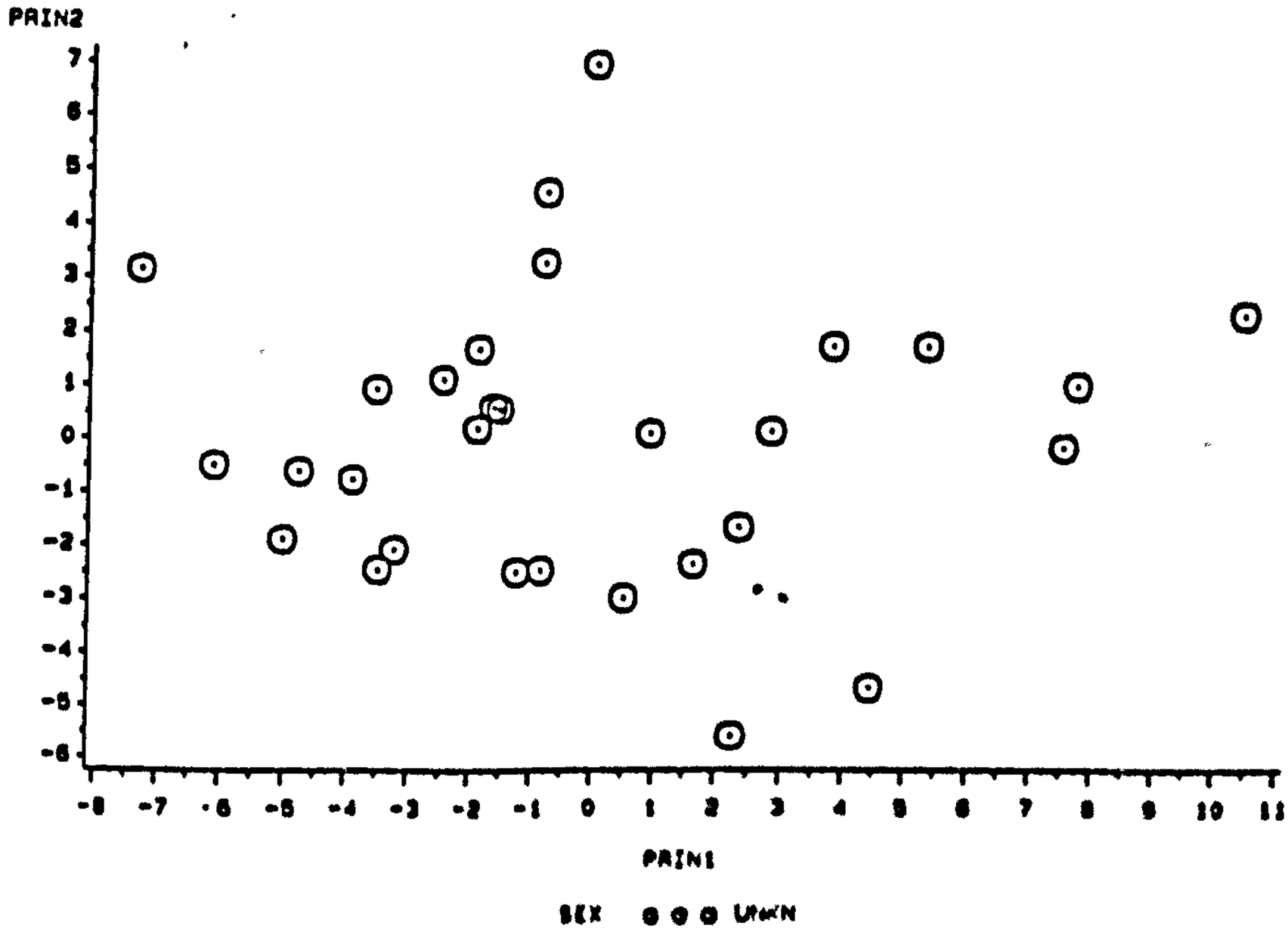
size dimorphism it appears that the caucasoids have a marginally greater sexual size difference than the chimpanzees. It may well be that this alone accounts for the clearer pattern of dimorphism shown on the first PC. From examination of tables 3.9 and 3.10, however, it is clear that size differences in *Pan* make a roughly similar (if not greater) relative contribution to overall within-group variability to that in the caucasoids.

The remaining human populations were of unknown sex distribution. PCA of their within population variability allowed no statements about sexual dimorphism to be made. Plots of PC I and II for each of the australoid, mongoloid, and negroid groups are presented in figures 3.5b, 3.6a, and 3.6b. From table 3.10 it can be seen that in all racial groups the scores of individuals on PC I correlated about 0.99 with their size. There does, however, seem to be a difference in the proportionate contribution of size to intra-racial variation. From table 3.9 it can be seen that size contributes 24% of intra-racial variability in caucasoids, 27% in mongoloids, 30% in negroids and 35% in australoids. The split in the distribution of individual australoids along PCI in figure 3.5b may well reflect a sexual difference consequent upon the greater proportion of size related within-group variability. It is particularly worth noting that the races of man differ in the proportion of their total variability which is size related despite the fact (table 3.6) that each of the racial samples in this study showed a similar size mean, range and variation.

FIGURE 3.6 – Principal Components Analysis of 59 raw linear and angular dimensions




a. Mongoloids




b. Negroids

Fig 3.6

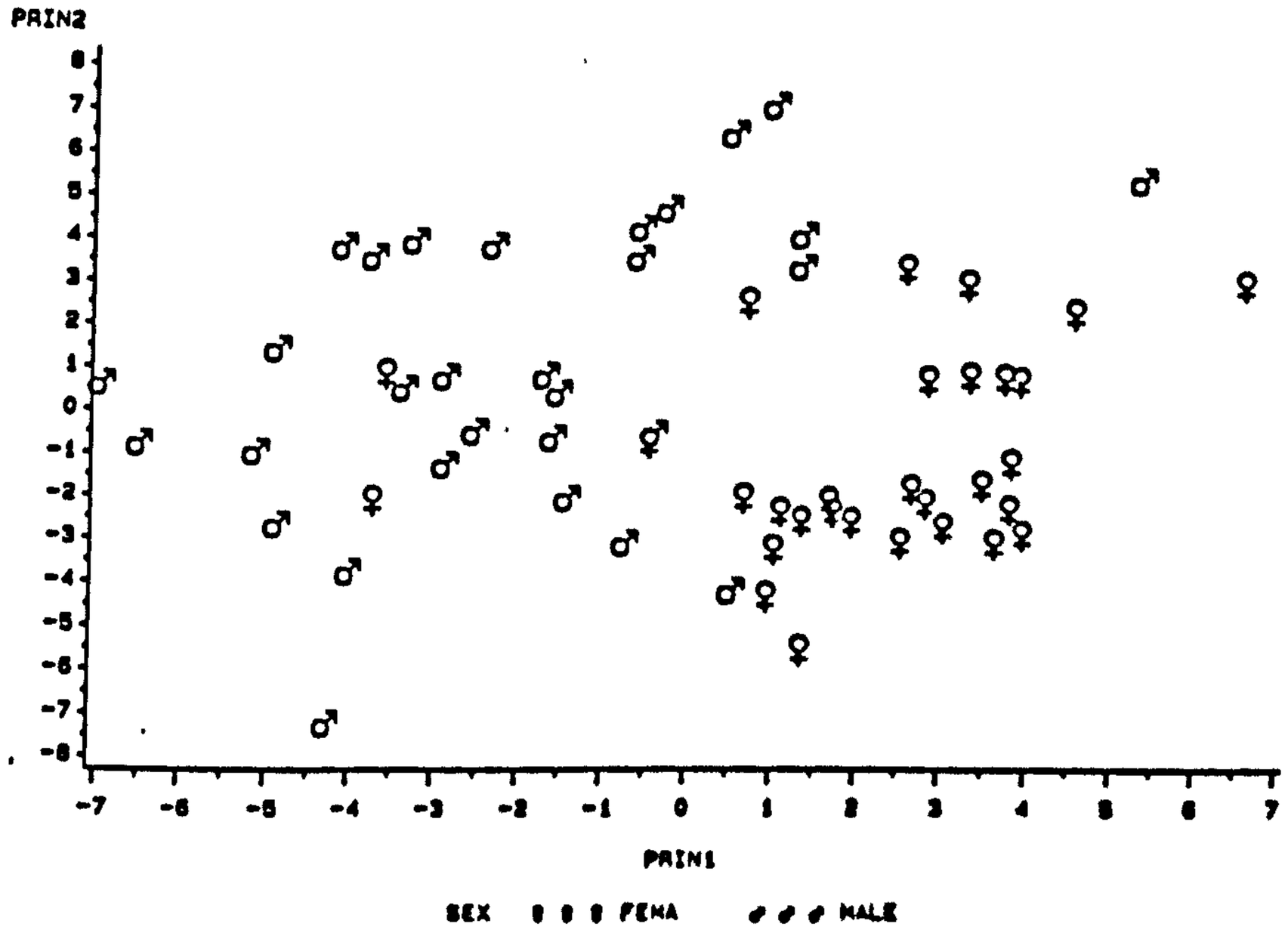
*PCA of the first 20 pairs of raw sine–cosine Fourier coefficients*

In figures 3.7 and 3.8 are illustrated plots of the first 2 and the first 3 principal components of the analyses using Fourier components from *Gorilla* and *Pongo*. These plots differ from the ones based upon raw linear and angular dimensions (discussed earlier) in that the separation of males and females is less marked and is not confined to PC I, PC II shows a proportion. This is better seen from the plots of PCs I+II+III (figure 3.8). It is reflected in the fact that the correlation of the scores of individuals with their size is more marked for PC II and higher PCs (table 3.12) than was the case in the analysis of linear dimensions.

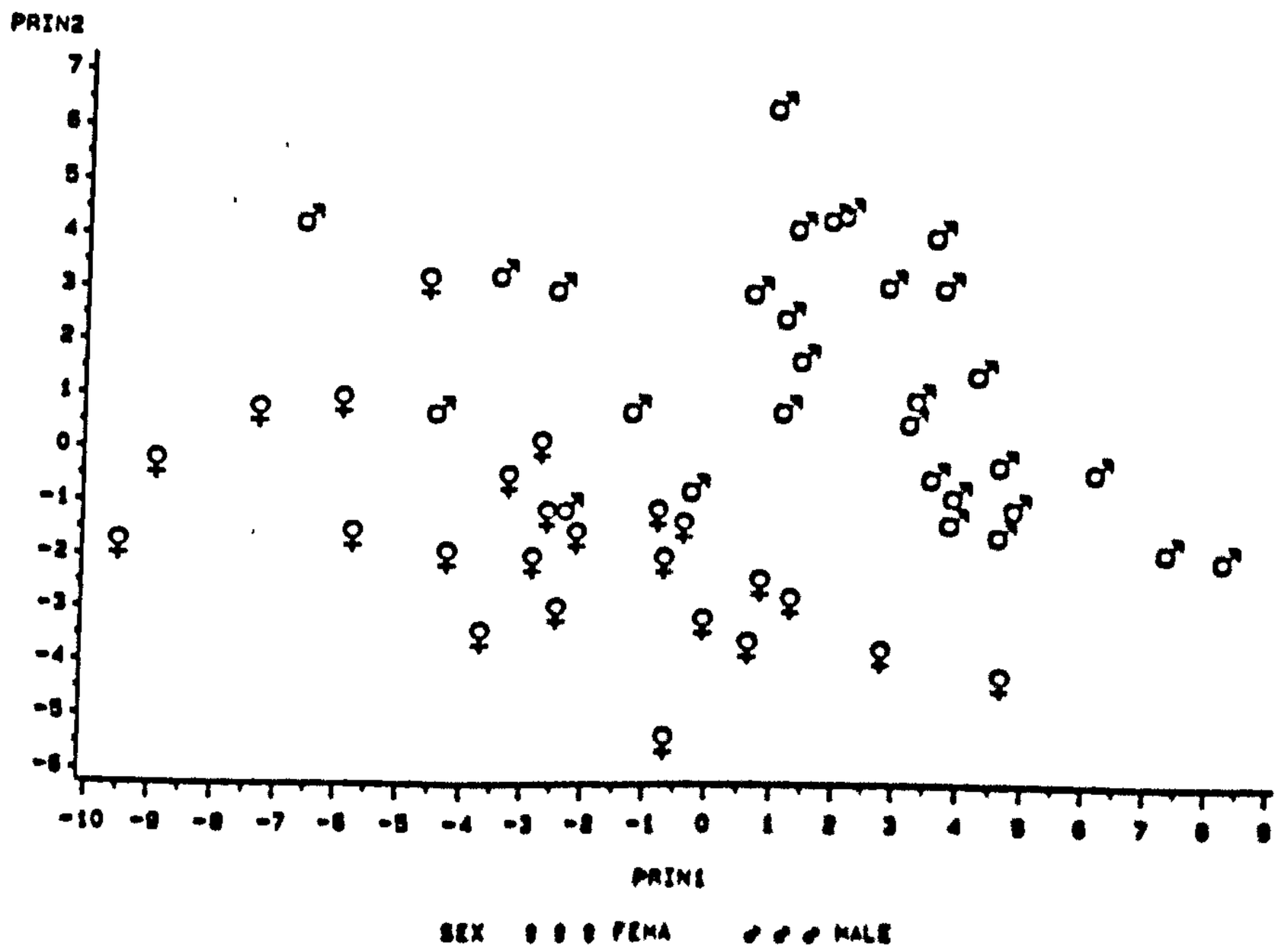
The principal component plots from *Pan* and the caucasoids (figures 3.9, 3.10 and 3.11a) fail to show any clear separation between males and females. Higher order principal components show moderate correlations with size (table 3.12) which in the case of the caucasoids are not significant (at $P<0.05$). This confirms the pattern of sexual dimorphism alluded to by the univariate analyses in which the number of significant correlations of size with the Fourier components was markedly reduced relative to the number of significant correlations observed within *Gorilla* and *Pongo*.

The principal component plots from analyses of the Fourier data within the racial groups of *Homo* (figures 3.11 and 3.12) show clouds of different shapes. In the negroids PC I ranges 14 SDU and PC II 14 SDU: the cloud is generally circular (n.b. axes drawn to different scales), in caucasoids PC I ranges 16 SDU and PC II 10 SDU, the cloud is more elliptical. This is coupled with a varying pattern of correlations of individual scores on PCs I – V with size (table 3.12).

FIGURE 3.7 – Principal Components Analysis of 20 raw sine/cosine Fourier coefficients



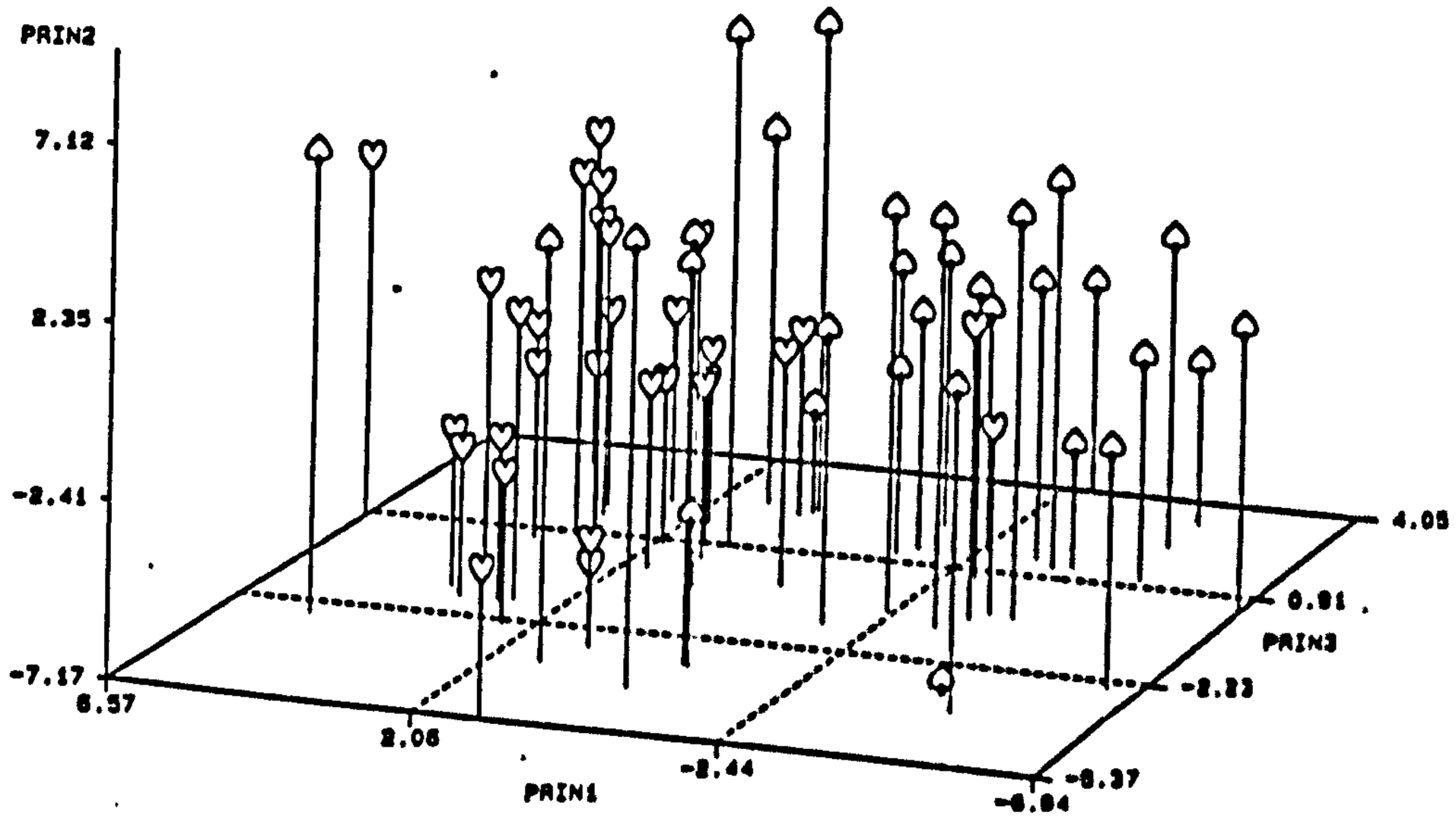

a. *Gorilla*



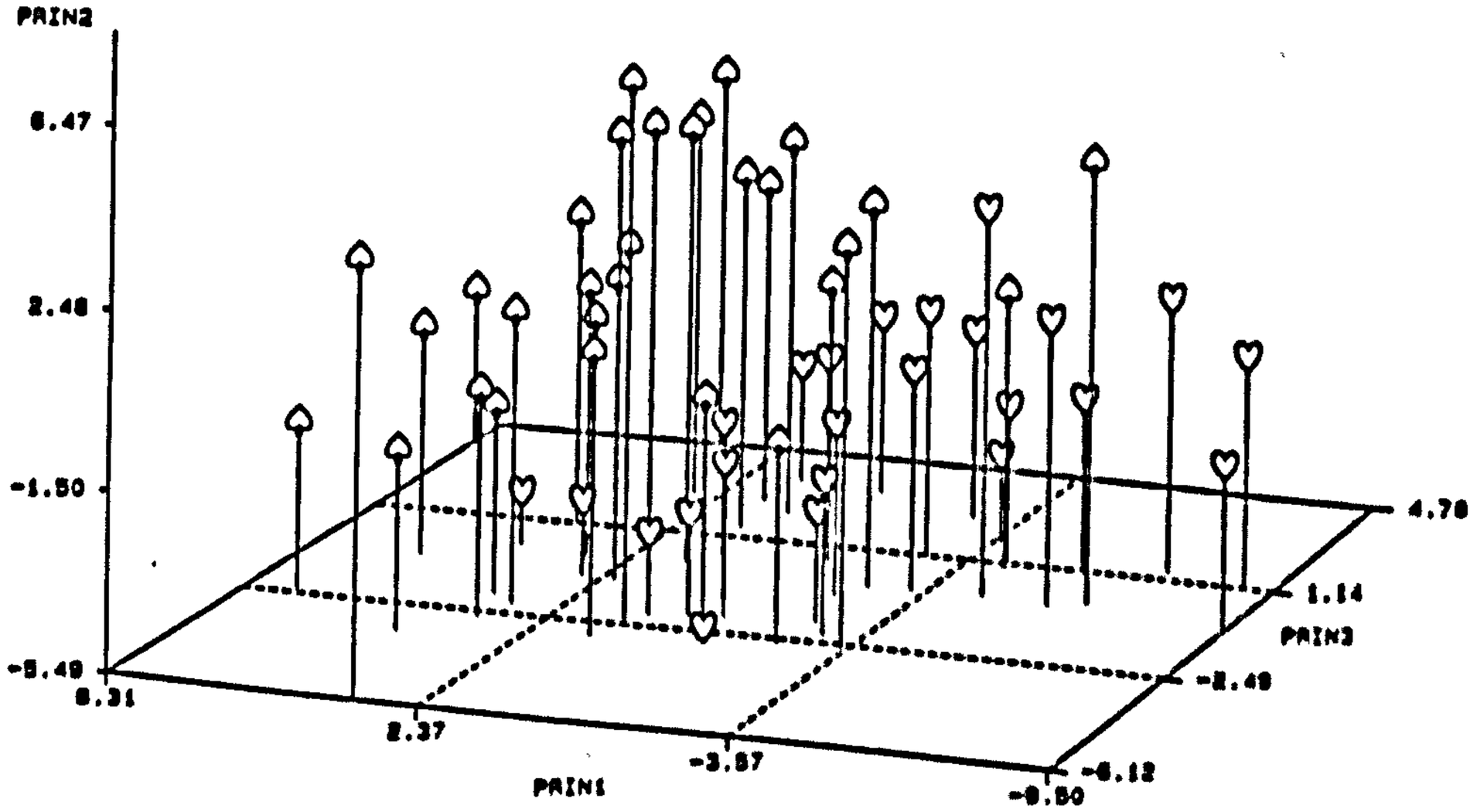

b. *Pongo*

Fig 3.7

FIGURE 3.8 – Principal Components Analysis of 20 raw sine/cosine Fourier coefficients



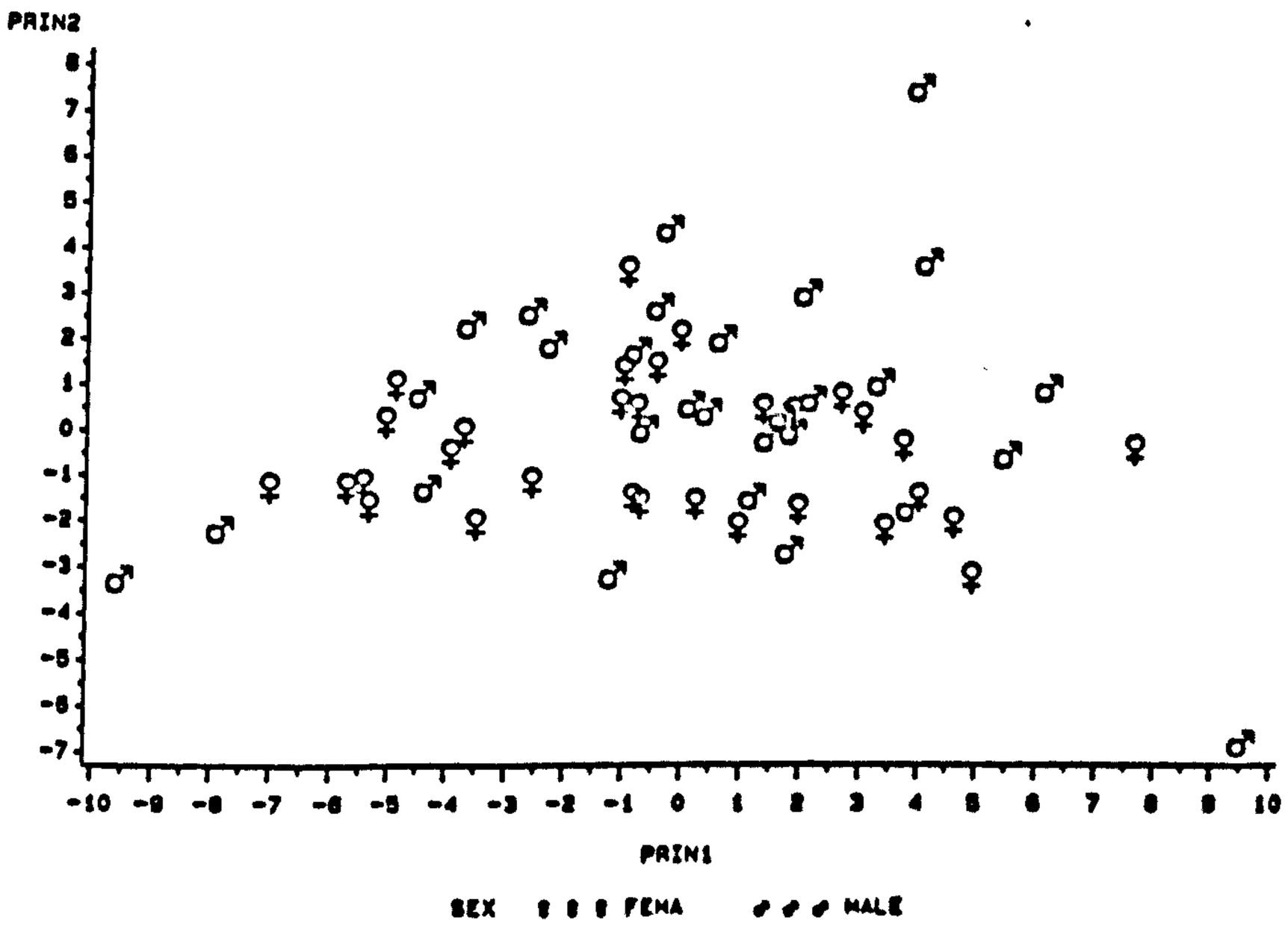

a. *Gorilla*




b. *Pongo*

Fig 3.8

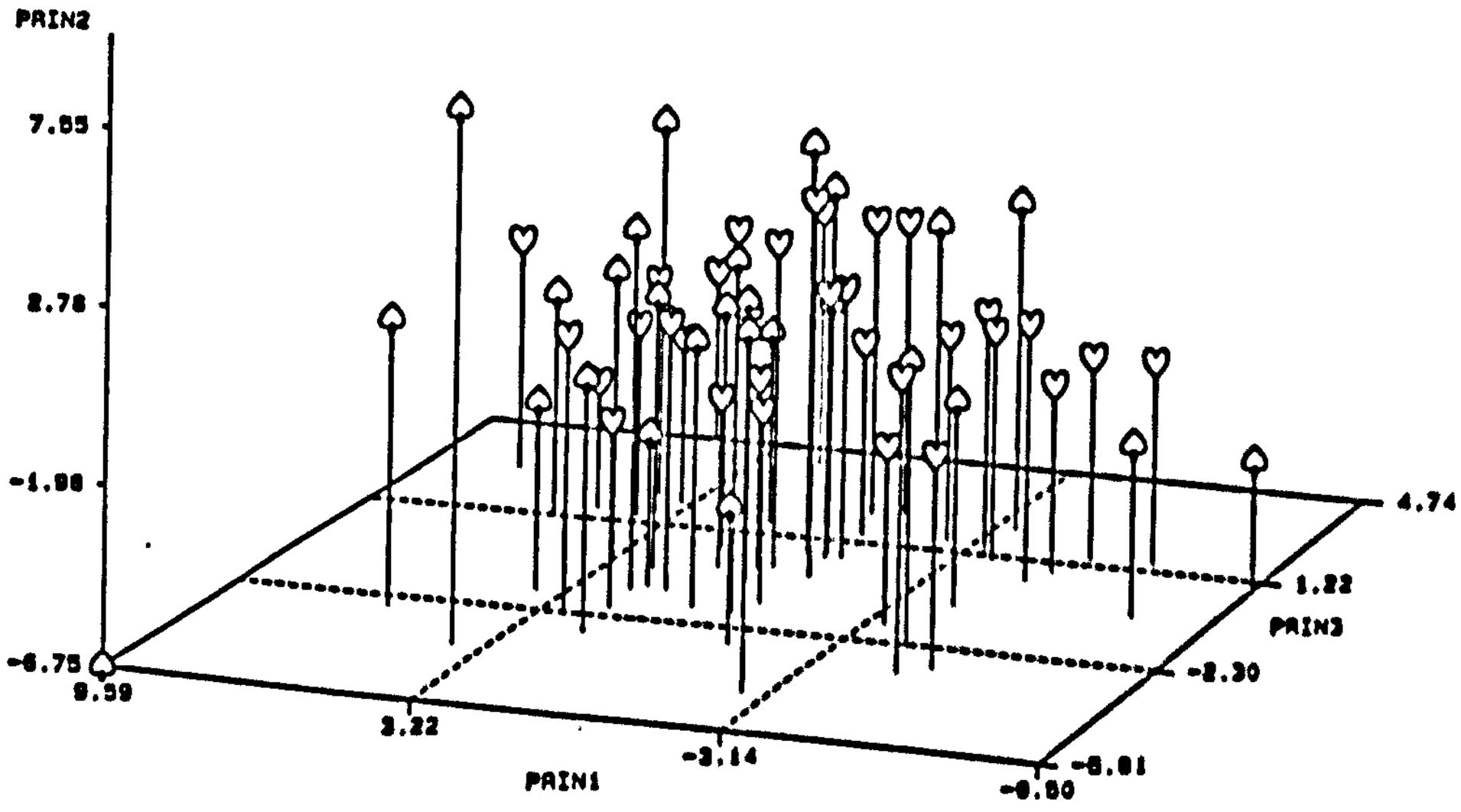
FIGURE 3.9 – Prinicipal Components Analysis of 20 raw sine/cosine Fourier coefficients



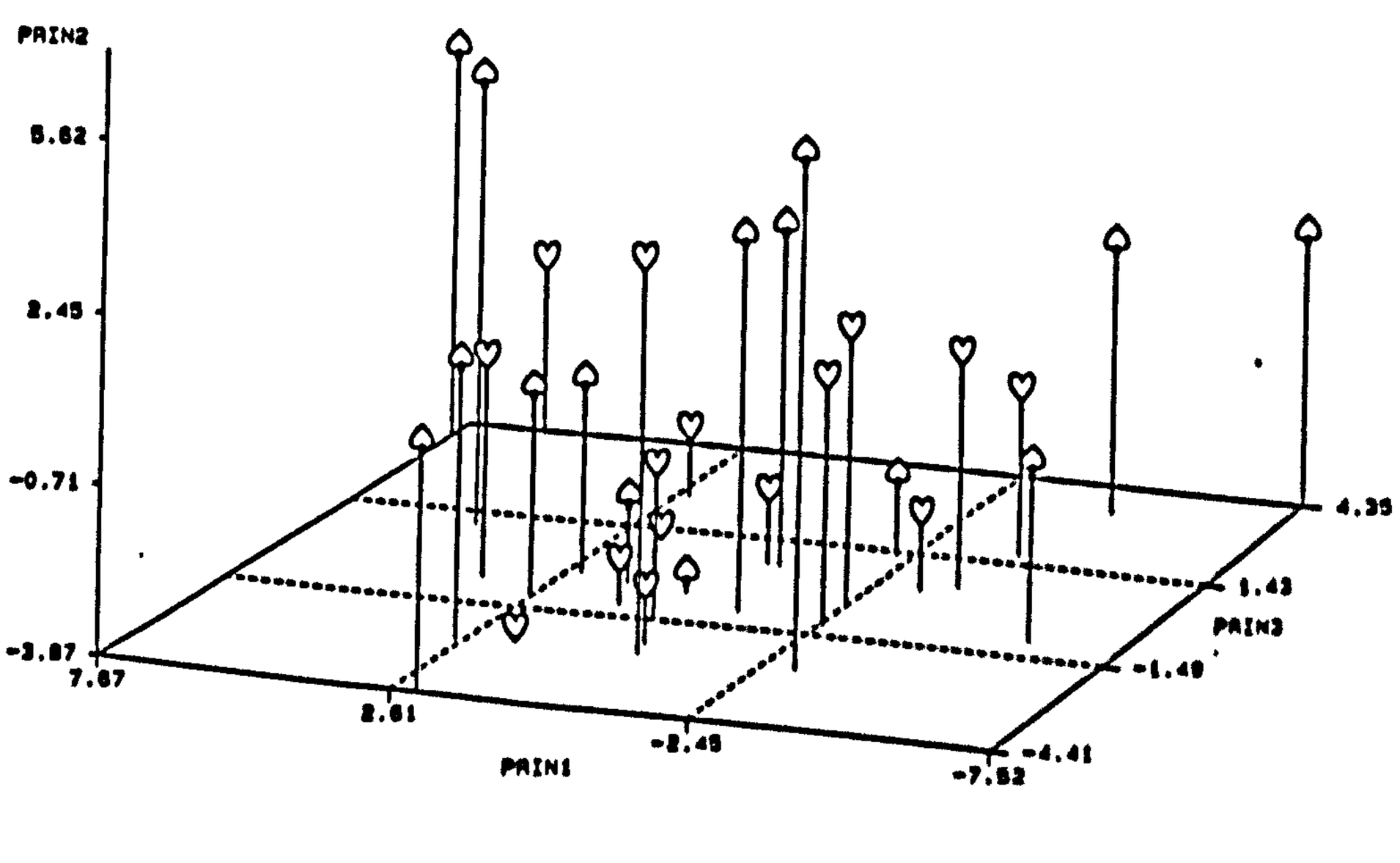

*Pan*

Fig 3.9

FIGURE 3.10 – Principal Components Analysis of 20 raw sine/cosine Fourier coefficients



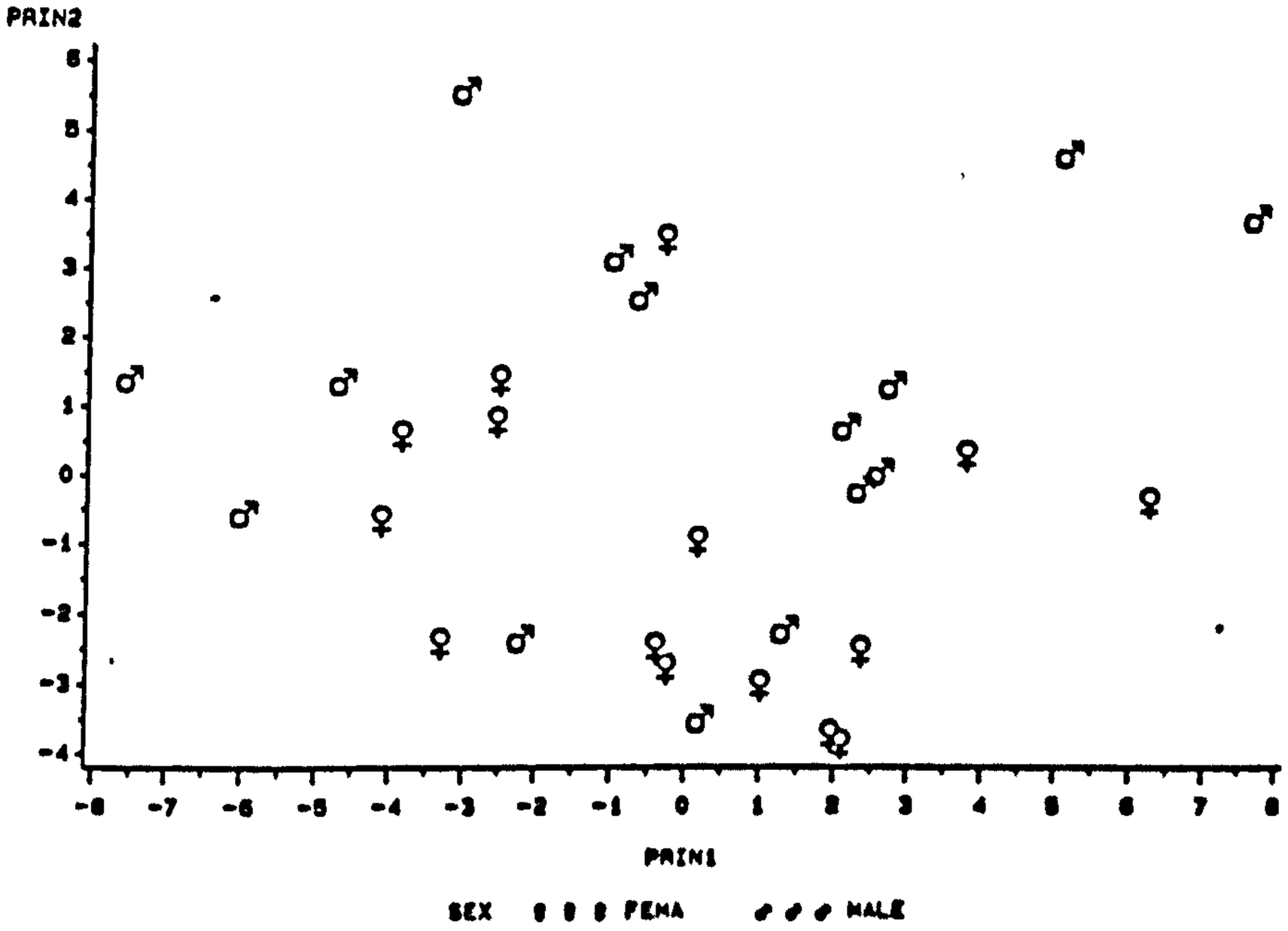

a. *Pan*



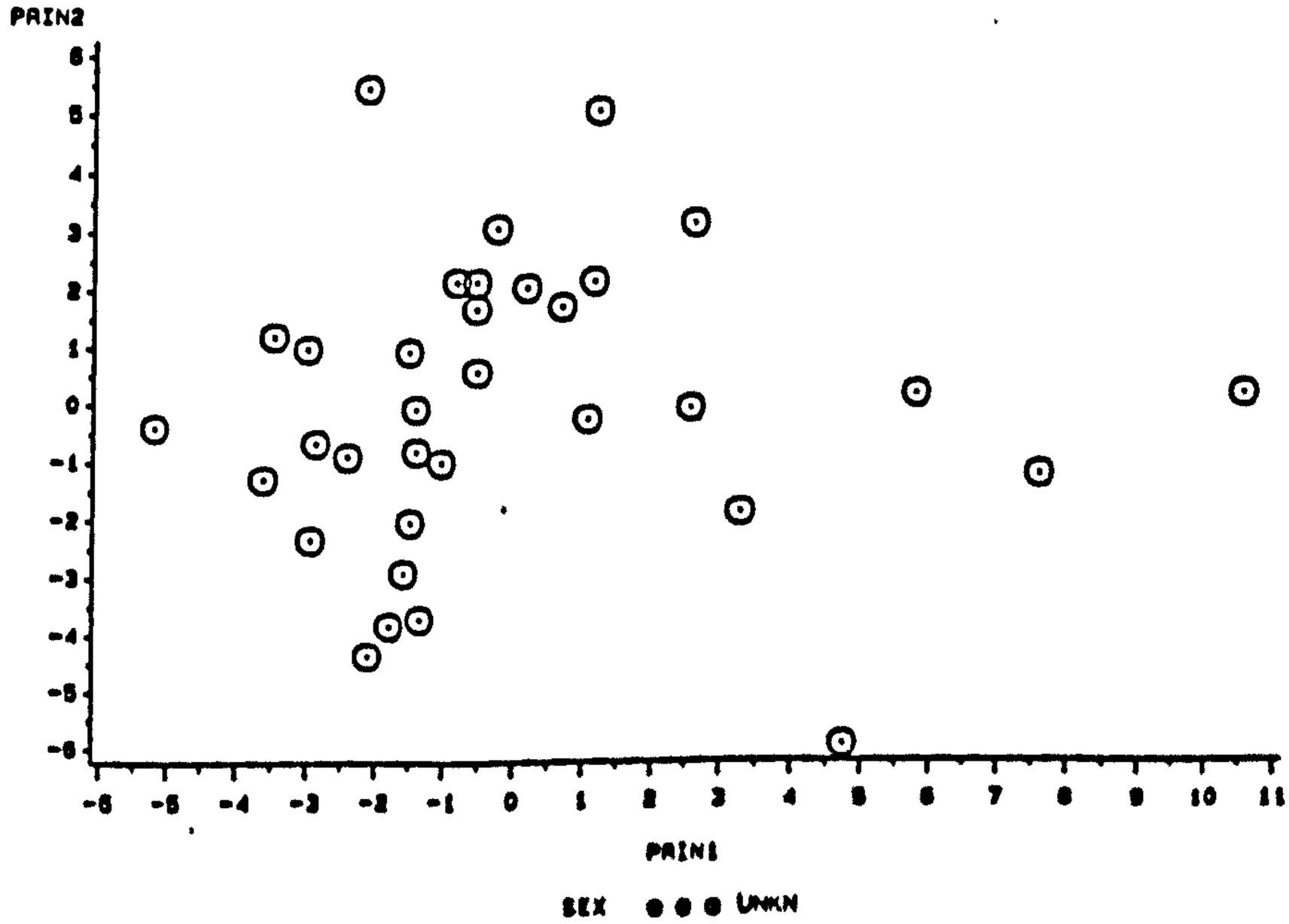

b. *Caucasoids*

Fig 3.10

FIGURE 3.11 – Principal Components Analysis of 20 raw sine/cosine Fourier Coefficients



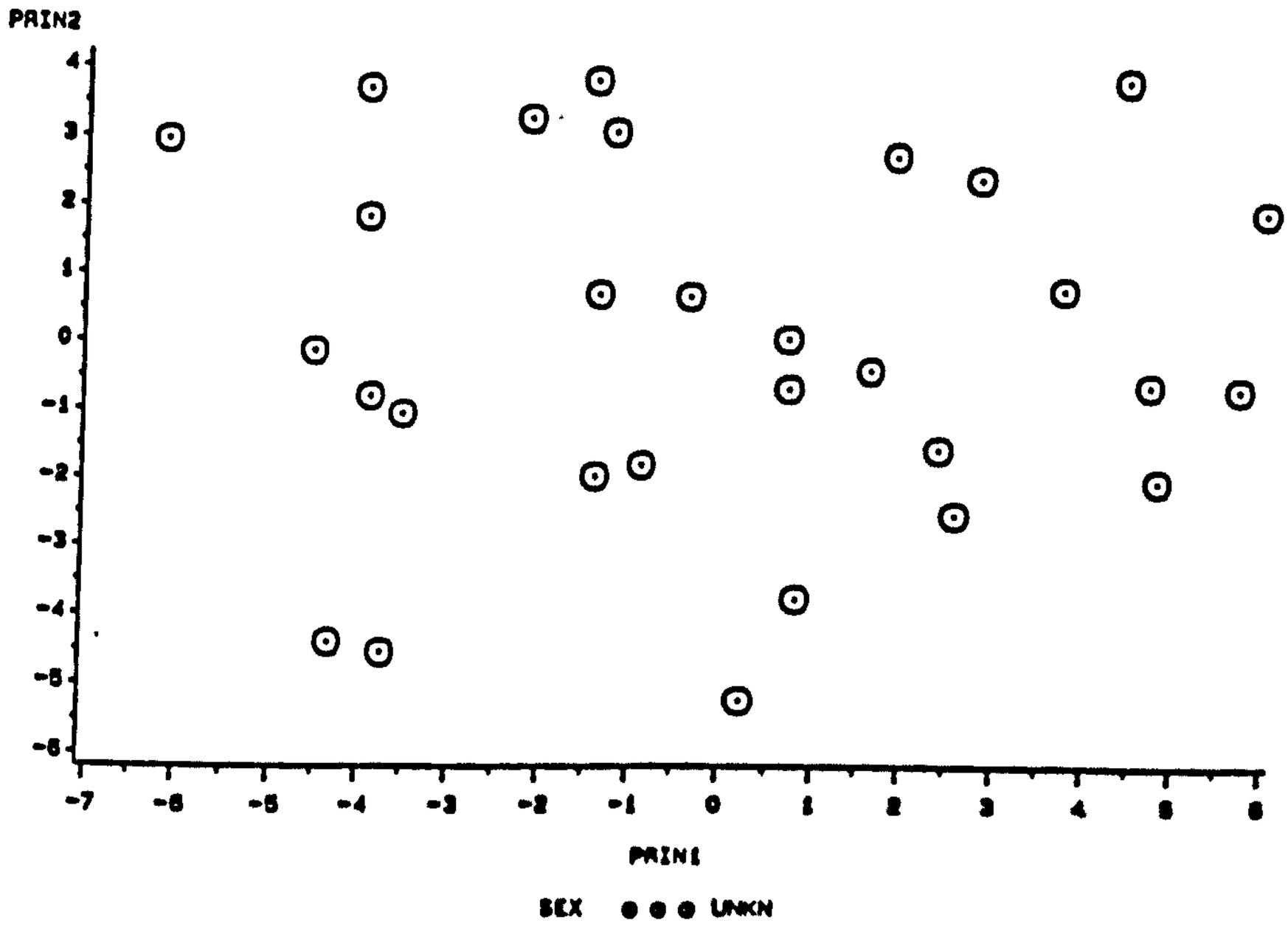

a. Caucasoids



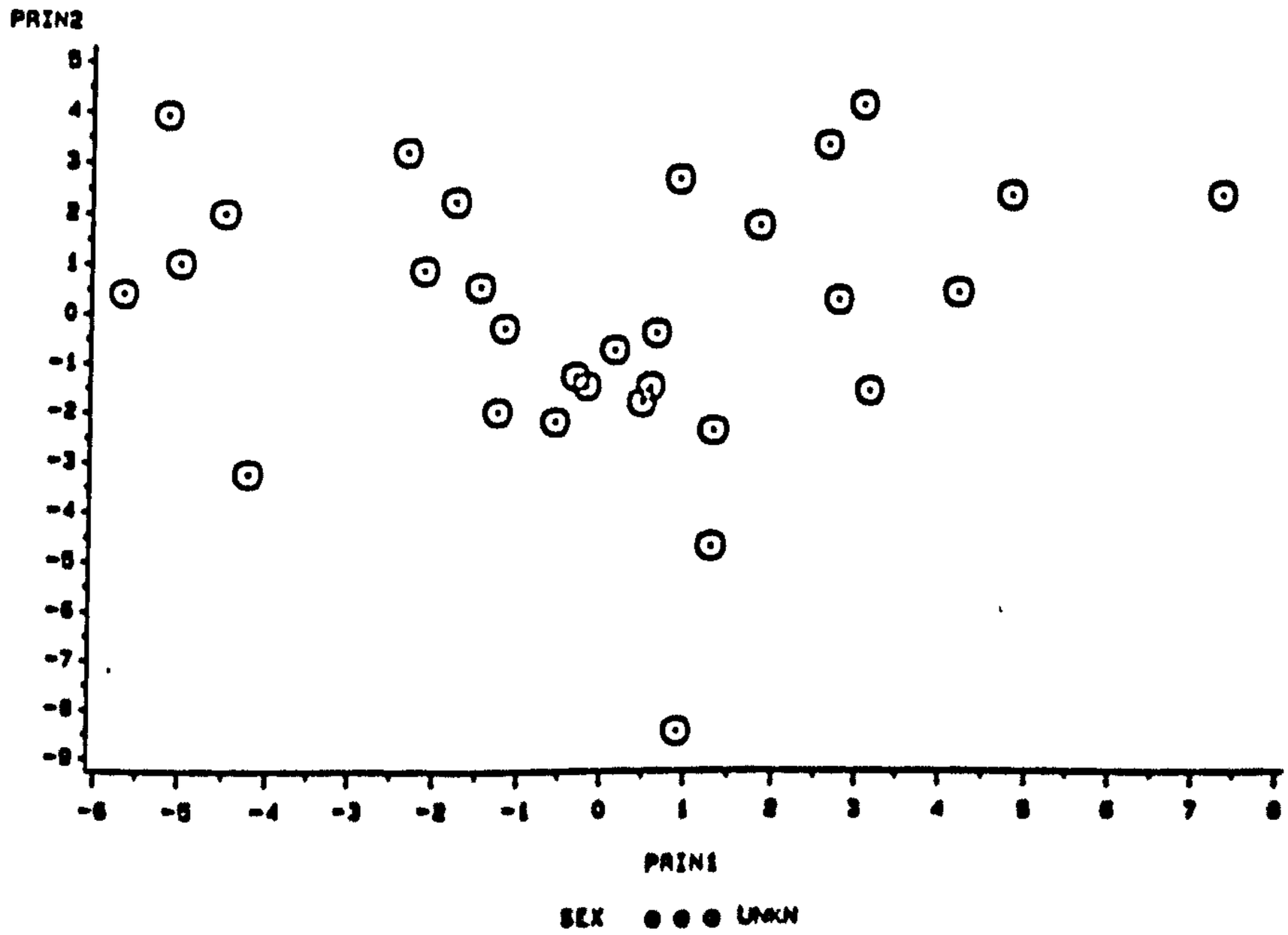

b. Australoids

Fig 3.11

FIGURE 3.12 – Principal Components Analysis of 20 raw sine/cosine Fourier Coefficients




a. Mongoloids




b. Negroids

Fig. 3.12

## TABLE 3.11

Principal Components Analysis of the first 20 raw sine-cosine Fourier coefficient pairs

| | Proportion (%) of total variance accounted for by the first n principal components (cumulative) | | | | |
|---|---|---|---|---|---|
| n = | 1 | 2 | 3 | 4 | 5 |
| group | | | | | |
| *Gorilla* | 26 | 50 | 61 | 70 | 75 |
| *Pongo* | 41 | 59 | 71 | 80 | 84 |
| *Pan* | 37 | 49 | 60 | 68 | 76 |
| *Homo:* | | | | | |
| Cauc. | 31 | 48 | 60 | 69 | 75 |
| Mon. | 29 | 46 | 57 | 66 | 72 |
| Neg. | 24 | 43 | 56 | 64 | 72 |
| Aust. | 28 | 44 | 57 | 65 | 73 |

## TABLE 3.12

Principal Components Analysis of the first 20 raw sine-cosine Fourier coefficient pairs

The correlation of the size variable (square root of area of midline tracing)

with the scores of individuals on PC no.:

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| *Gorilla* | −0.59** | 0.47** | 0.0 | 0.43** | 0.02 |
| *Pongo* | 0.54** | 0.58** | −0.09 | −0.15 | −0.05 |
| *Pan* | 0.00 | 0.22 | −0.27* | 0.09 | −0.27* |
| *Homo:* | | | | | |
| Cauc. | 0.07 | 0.14 | 0.09 | 0.26 | 0.09 |
| Mon. | 0.35* | 0.12 | 0.08 | 0.45 | −0.25 |
| Neg | 0.35* | 0.02 | 0.55* | 0.16 | 0.37* |
| Aust. | 0.25 | 0.52** | 0.22 | 0.12 | −0.24 |

P < 0.01 = **

P < 0.05 = *

The overall impression is one of differing patterns of variability and of differing size influences on shape. These size influences are often reflected in higher PCs and are therefore not clear from the plots of PCs (figs. 3.11 and 3.12).

The PCAs of Fourier data have agreed with those of linear and angular dimensions in indicating that a major component of the within-group variation in *Gorilla* and *Pongo* is size related and in showing that size has a proportionately smaller influence on within-group variation in *Pan* and *Homo*. A further point of agreement is that both sets of PCAs have indicated that there are differences between the racial groups of *Homo* in the proportion and pattern of total within-group variance which is influenced by size.

The two sets of analyses disagree, however, in the ways in which they have been influenced by size. The influence of size on the scores of individuals on PC I is markedly reduced in the analyses of Fourier data.

The difference in result implies that in the analysis of Fourier data shape differences which are not size related are relatively more important. This difference may be a consequence of the fact that the Fourier coefficients are derived from just the midline projection, whereas the linear and angular measurements cover a much wider anatomical scope. Considering that the midline projections show a considerable size variation, however, it is unclear how this difference in scope could have resulted in the observed degree of disagreement.

A further reason for the difference may be that the Fourier data are fundamentally different to the linear and angular dimensions. Each Fourier component, unlike each linear dimension, does not represent the absolute size

of a particular dimension. In Fourier data the magnitude of the first cosine component (cosine 0) is directly proportional the square root of the midline area of each cranium.

In these analyses cosine 0 has been omitted because it is a "pure size" rather than a shape variable and to have included it would have been equivalent to including the size variable in the analyses of linear and angular measurements.

Every remaining Fourier component reflects shape more than size though size still influences each. This is because in the raw data the midline areas of the crania are unequal and each component represents the magnitude of a wave of a particular frequency which must be added to the circle defined by cosine 0 (see chapter 2).

In the univariate studies the fact that the Fourier components of order greater than 0 are less size dependent than linear dimensions is reflected in the generally lower correlations observed between Fourier components and the size variable than was observed between linear dimensions and the size variable. The result is that shape variations which are not size related have a more pronounced influence in the PCAs.

## II. Scaled data

The previous analyses have indicated that size differences contribute a significant proportion of within-group variability in all of the hominoids in this study. These differences may be of two types: simple geometric scale differences or more complex differences in scale and in form such that larger individuals tend to have a different shape.

In order to investigate the relative contributions of scale and scale plus shape changes to the patterns of within-group variability a series of analyses of geometrically scaled data were undertaken.

To allow a greater degree of comparability between the analyses using linear and angular measurements and those using Fourier coefficients only those 25 measurements taken from or projected onto the midline were used. The linear dimensions were scaled according to the square root of the midline area of each cranium, angles were unaltered, whilst the Fourier data were scaled by making all midline tracings have equal area.

*PCAs of 25 scaled linear and angular dimensions*

Plots of the scores of *Gorilla* and *Pongo* on PC I and II are given in figure 3.13. Despite the fact that simple size differences between individuals have been removed there is a clear difference between the scores of males and females on PC I whilst PC II shows no sexual difference. From table 3.14 it can be seen that in these two groups there is a correlation of just over 0.73 ($P<0.01$) between the size of individuals and their scores on PC I although the data have been adjusted for simple scale differences. The dimorphism shown along this first PC is principally a size related shape dimorphism. This shape dimorphism accounts for about a third of the total within-group shape variability (see table 3.13).

Comparison of these plots with those of the PCAs of the other groups in which sex was known, *Pan* and the caucasoids (figures 3.14 and 3.15a), demonstrates that within the latter two groups shape contrasts between the sexes

## TABLE 3.13

**Principal Components Analysis of 25 scaled linear and angular dimensions from the midline**

**Proportion (%) of total variance accounted for by the first n principal components (cumulative)**

| n = | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| group | | | | | |
| *Gorilla* | 36 | 49 | 60 | 68 | 73 |
| *Pongo* | 31 | 48 | 59 | 69 | 77 |
| *Pan* | 25 | 43 | 57 | 67 | 74 |
| *Homo:* | | | | | |
| Cauc. | 24 | 41 | 54 | 66 | 75 |
| Mon. | 22 | 43 | 60 | 68 | 75 |
| Neg. | 22 | 42 | 56 | 65 | 73 |
| Aust. | 21 | 37 | 51 | 63 | 71 |

## TABLE 3.14

**Principal Components Analysis of 25 scaled linear and angular dimensions**

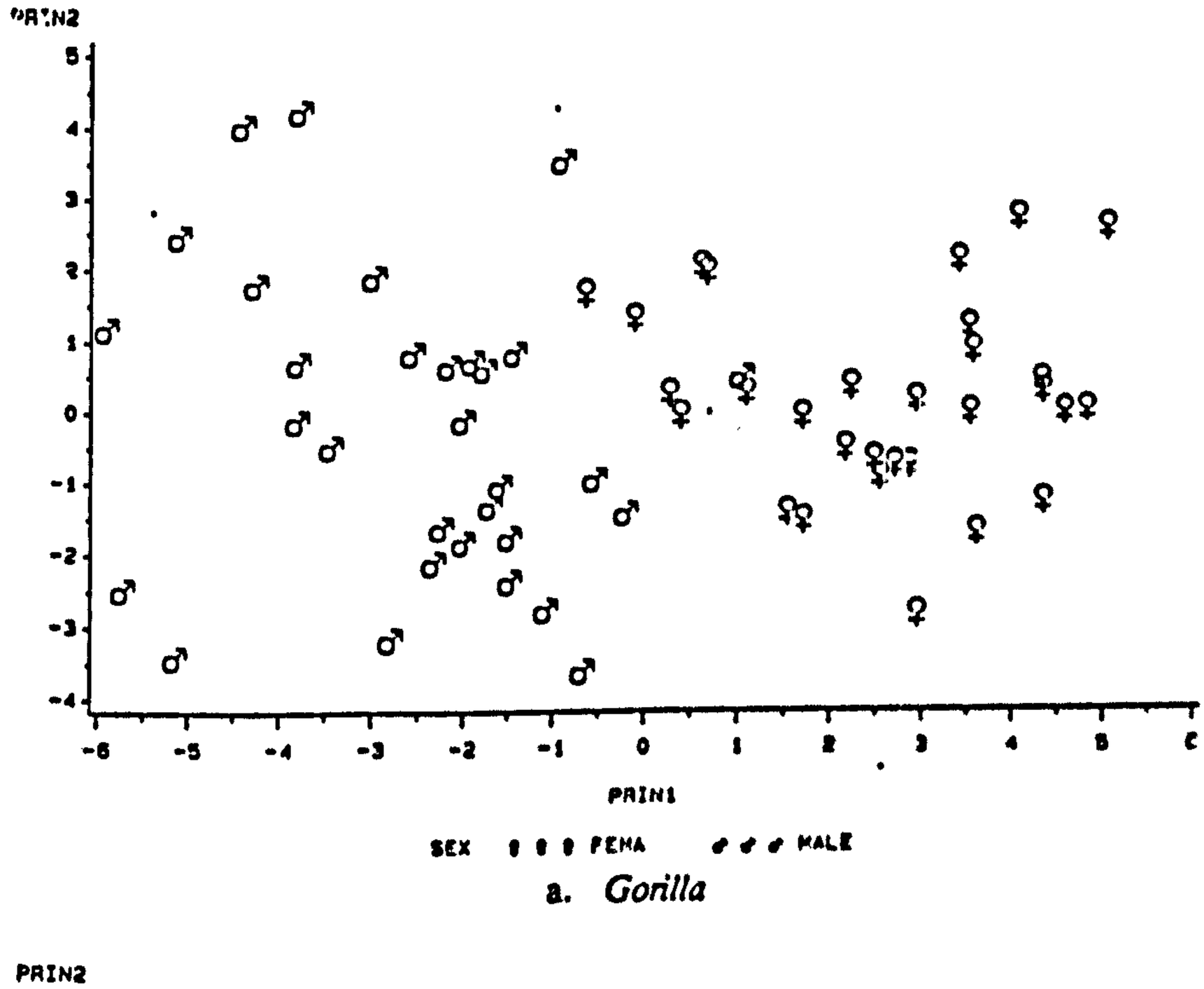
**The correlation of the size variable (square root of area of midline tracing) with the score of individuals on PC no:**

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| *Gorilla* | −0.74** | −0.09 | −0.10 | −0.18 | 0.25* |
| *Pongo* | 0.73** | −0.19 | 0.10 | −0.11 | 0.05 |
| *Pan* | 0.17 | −0.21 | −0.11 | 0.00 | 0.01 |
| *Homo*: | | | | | |
| Cauc. | −0.12 | 0.10 | −0.34(*) | 0.02 | 0.22 |
| Mon. | −0.36* | 0.36* | 0.18 | −0.06 | 0.02 |
| Neg. | 0.22 | 0.21 | −0.14 | 0.26 | 0.32 |
| Aust. | −0.13 | −0.31 | −0.27 | 0.30 | −0.19 |

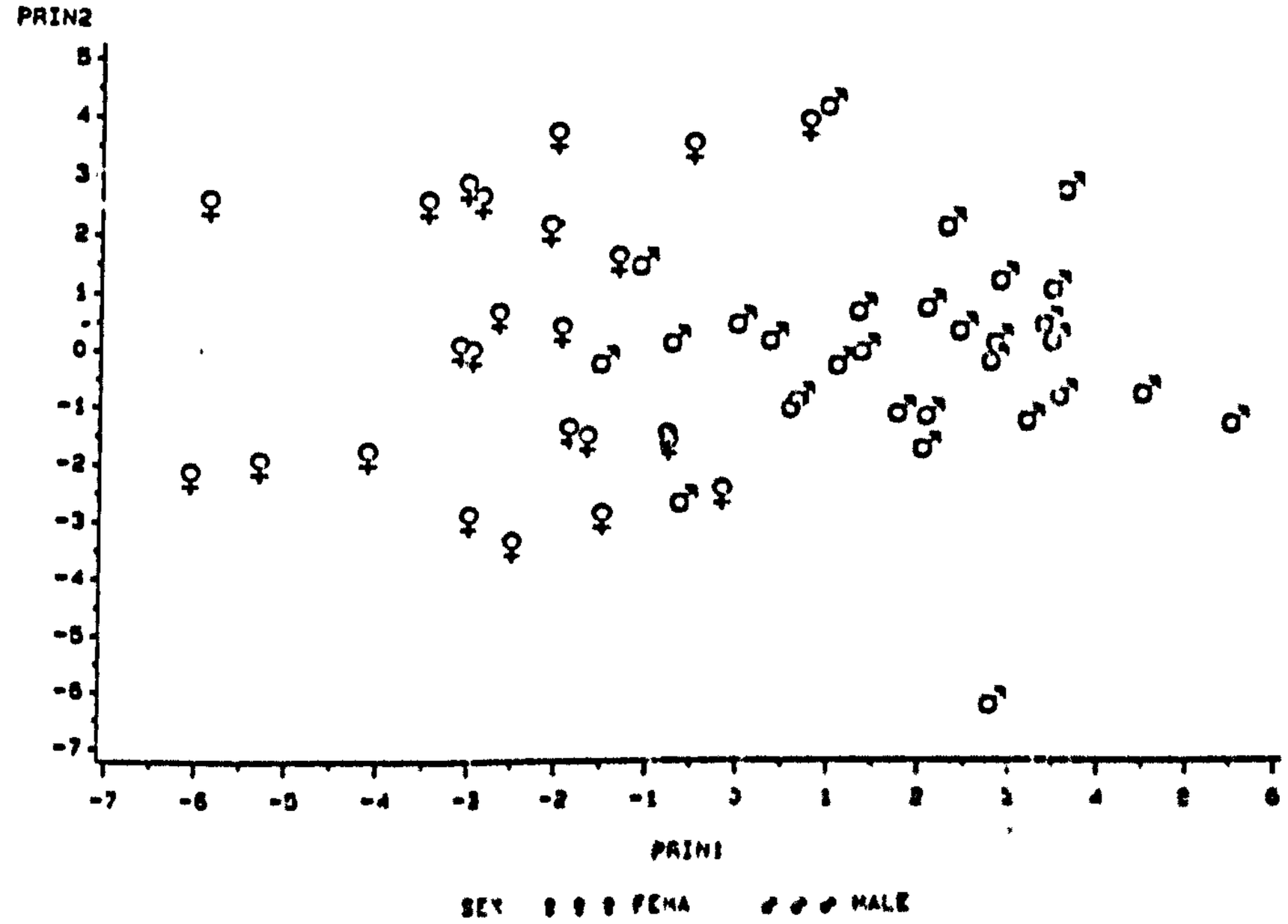
$P < 0.01$ = **

$P < 0.05$ = *

FIGURE 3.13 – Principal Components Analysis of 25 scaled linear and angular dimensions from the midline



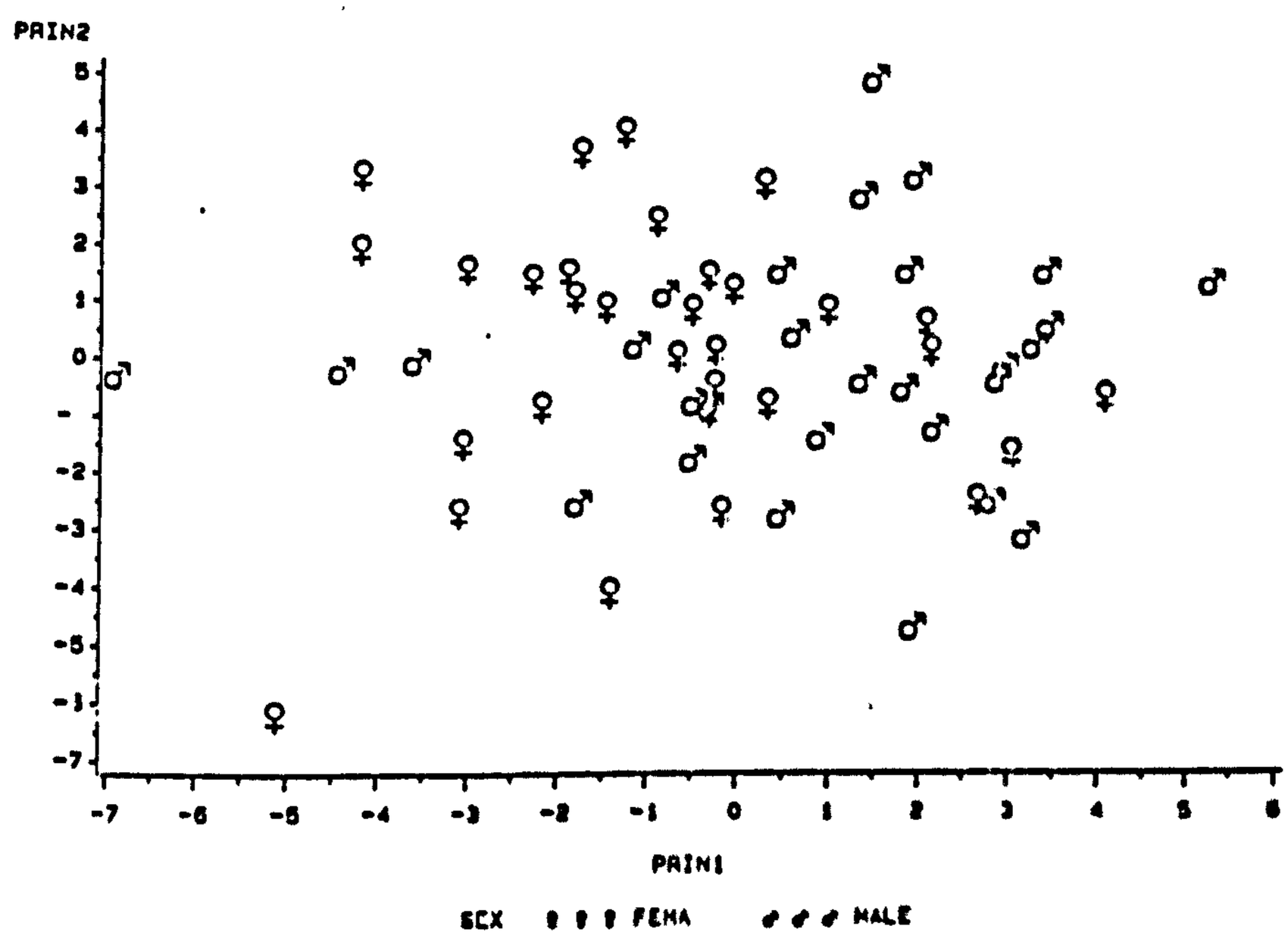

a. *Gorilla*




b. *Pongo*

Fig 3.13

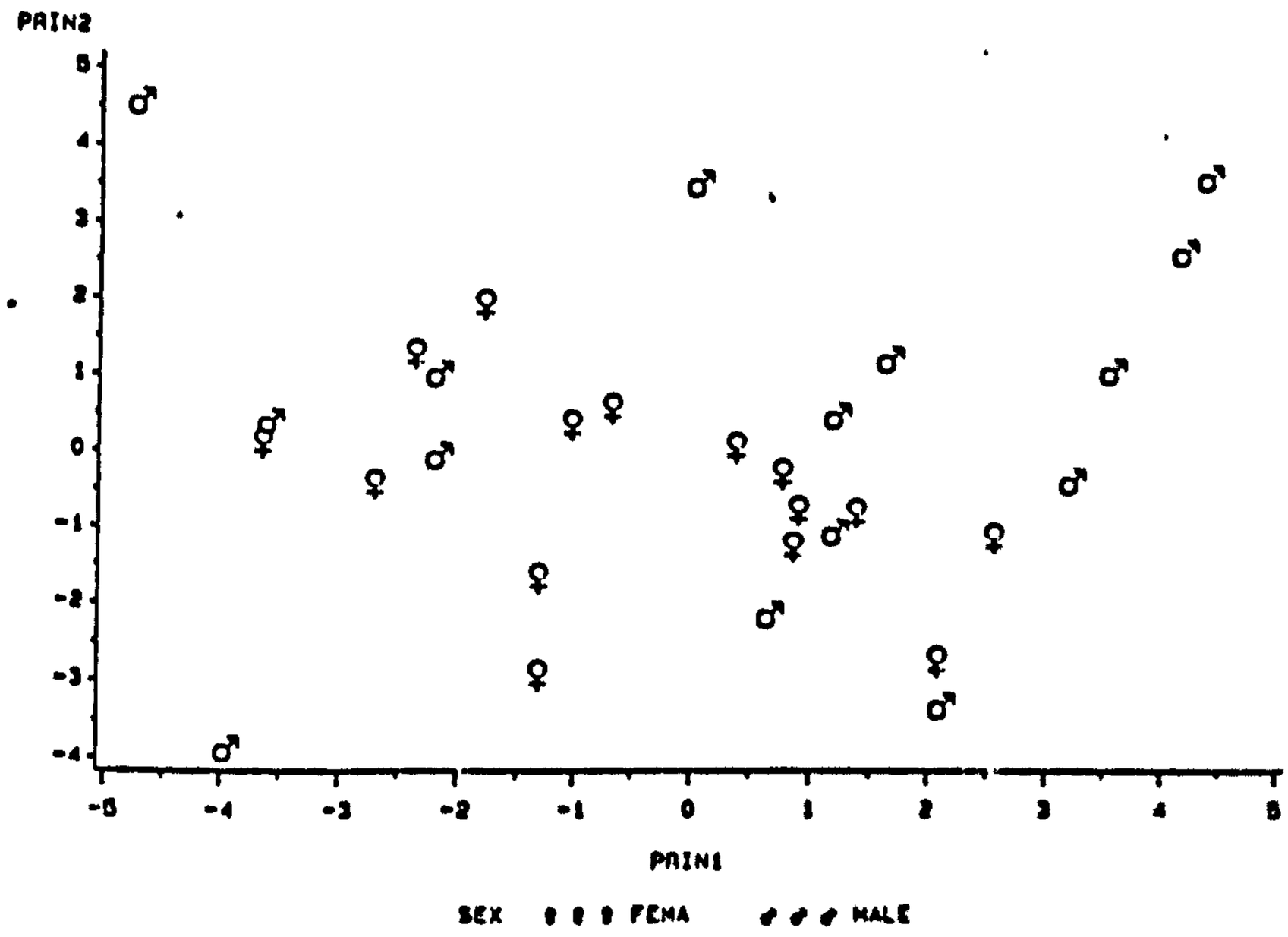
FIGURE 3.14 – Principal Components Analysis of 25 scaled linear and angular dimensions from the midline



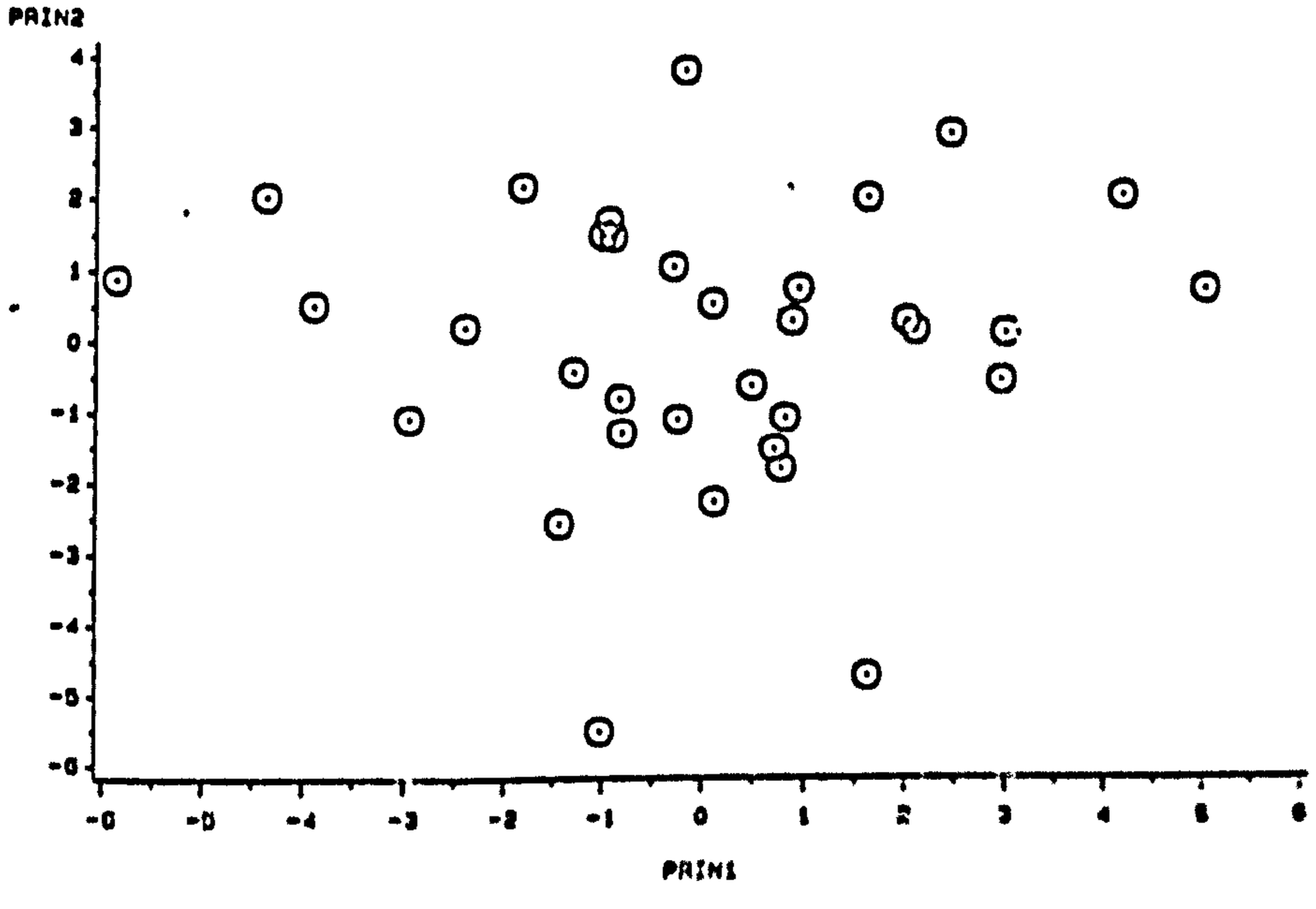

*Pan*

**Fig 3.14**

FIGURE 3.15 – Principal Components Analysis of 25 scaled linear and angular dimensions from the midline



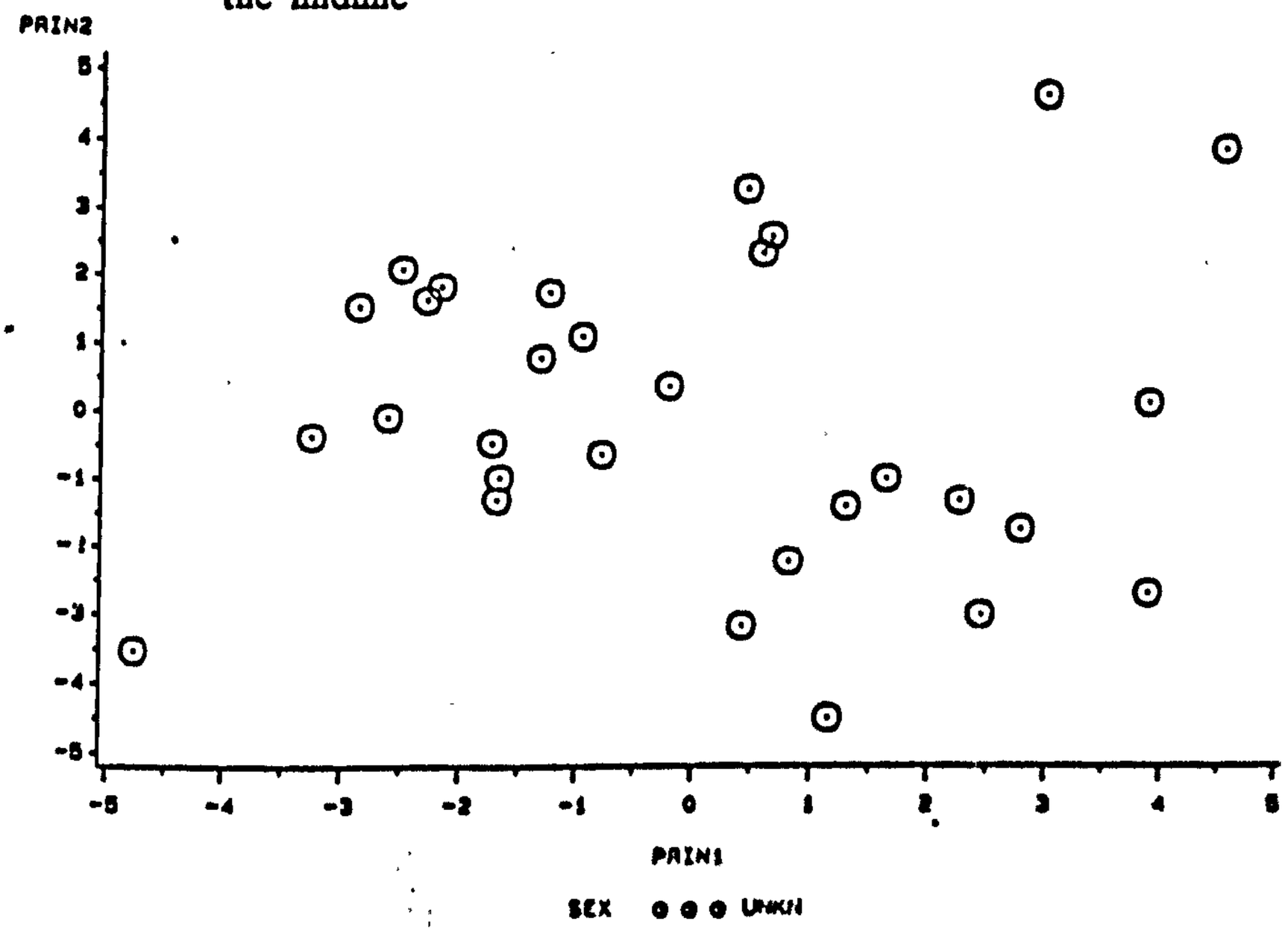

a. Caucasoids



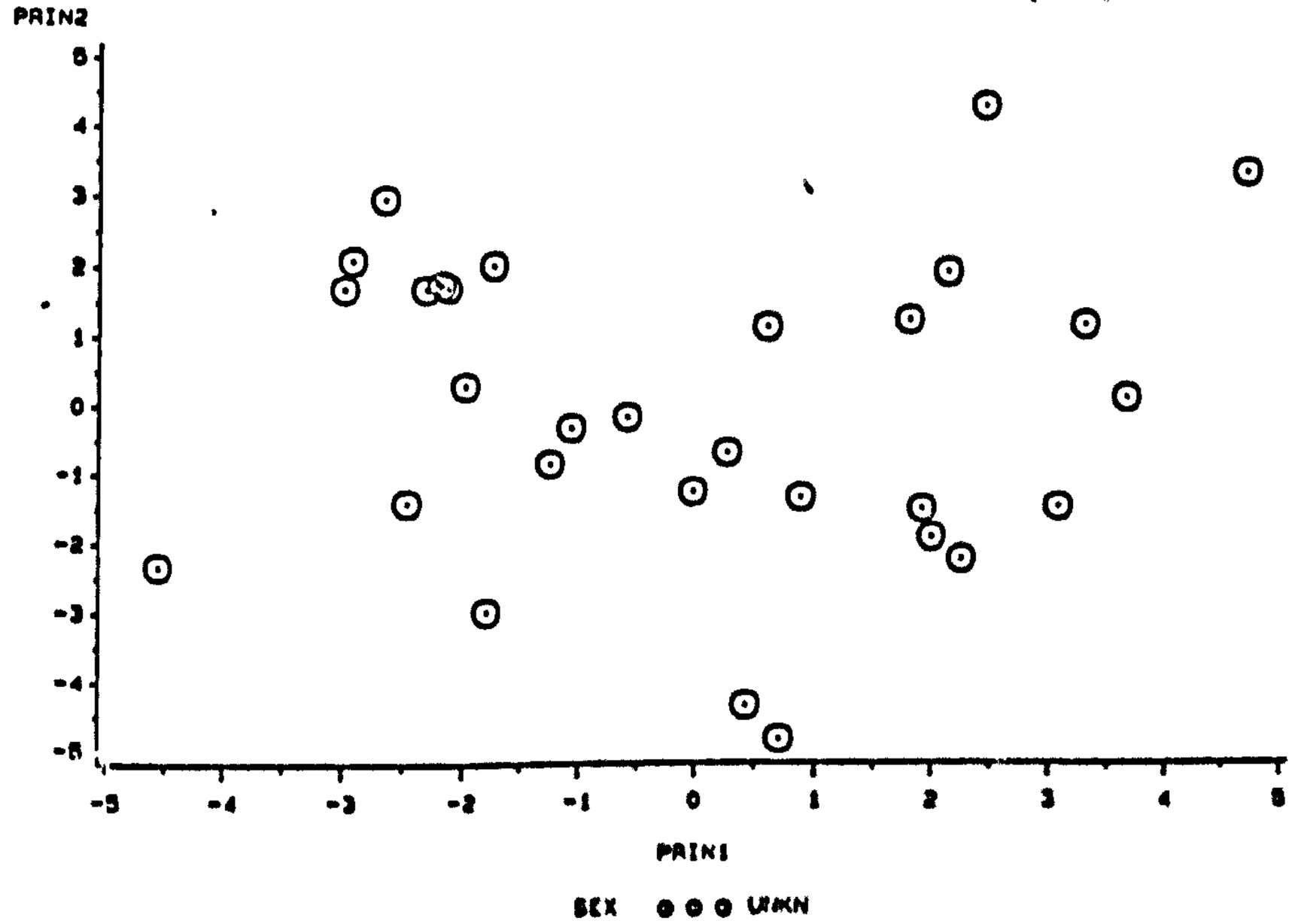

b. Australoids

Fig 3.15

FIGURE 3.16 – Principal Components Analysis of 25 scaled linear and angular dimensions from the midline




a. Mongoloids




b. Negroids

Fig 3.16

are less. The correlation of the size of individuals with their scores on PC I is small and insignificant (table 3.14). There is, however, a greater correlation of size with scores on higher PCs in both groups (though only that on PC III in the caucasoids is significant, $r = -0.34$, $P < 0.05$). It seems that sexual shape contrasts are reduced relative to other sources of within-group variability. This difference in sexual shape contrast is consistent with the absolutely and relatively smaller size contrast between the sexes in these groups (table 3.17).

The plots of the scores of individuals on PCs I and II in the human racial groups (figures 3.15 and 3.16) indicate a relative contraction of within-group variability as judged by the lengths of the first PCs (compare with figs. 3.5 and 3.6).

The pattern of correlations of PC scores with size (though these are relatively small and mostly insignificant) varies between the human groups. This contrasts with the proportions of total within-group variation expressed by each PC which are roughly constant (table 3.13). These findings suggest that there are differences in the patterns of size/shape relationships between the human racial groups.

*PCA of the first 20 pairs of scaled sine-cosine Fourier coefficients*

The first two principal components from the analysis of scaled Fourier data in *Gorilla* and *Pongo* are plotted in figure 3.17. These plots differ markedly from the ones based upon scaled linear and angular dimensions (figure 3.13) and less so from the ones based upon raw Fourier components (figure 3.7) in that the separation of males and females is less marked.

The plots of PC I and II from the analyses of intra-group variation in *Pan* and the caucasoids (figures 3.18 and 3.19a) fail to show any clear separation between males and females. Higher order principal components show moderate correlations with size (though they are insignificant, $P<0.05$, in the caucasoids, table 3.16). This confirms the pattern of sexual dimorphism alluded to by the earlier analyses.

In common with the studies of raw Fourier components the principal component plots from analyses of the scaled Fourier data within the racial groups of *Homo* (figures 3.19 and 3.20) show clouds of different shapes. This is again coupled with a varying pattern of correlations of individual scores on PCs I-V with size (table 3.16) and the overall impression is one of differing patterns of variability and of differing size influences on shape.

The reduction in the degree of sexual separation between the analyses using raw and those using scaled Fourier data is consistent with the general, though moderate, reduction in the correlations of the scores of individuals on PCs with the size variable (compare tables 3.12 and 3.16). This relates to a reduction in the influence of scale on the Fourier data. A further possible effect of the reduction in the influence of scale is the marginal reduction in the proportions of total within-group variance which are accounted for by successive PCs relative to the study of raw Fourier coefficients (compare tables 3.15 and 3.11). Non-size related aspects of variation (i.e. shape variation) are proportionately more important and these are more dependent on higher PCs to account for them.

The differences between the analyses of scaled linear and angular measurements and those of scaled Fourier data in the extent of sexual separation

## TABLE 3.15

Principal Components Analysis of the first 20 scaled sine–cosine Fourier coefficient pairs

| | Proportion (%) of total variance accounted for by the first n principal components (cumulative) | | | | |
|---|---|---|---|---|---|
| n = | 1 | 2 | 3 | 4 | 5 |
| group | | | | | |
| *Gorilla* | 25 | 47 | 59 | 66 | 72 |
| *Pongo* | 39 | 55 | 66 | 76 | 80 |
| *Pan* | 37 | 49 | 59 | 68 | 74 |
| *Homo:* | | | | | |
| Cauc. | 31 | 47 | 59 | 67 | 73 |
| Mon. | 28 | 46 | 56 | 64 | 70 |
| Neg. | 23 | 42 | 54 | 63 | 70 |
| Aust. | 27 | 43 | 55 | 64 | 71 |

## TABLE 3.16

**Principal Components Analysis of the first 20 scaled sine–cosine Fourier coefficient pairs**

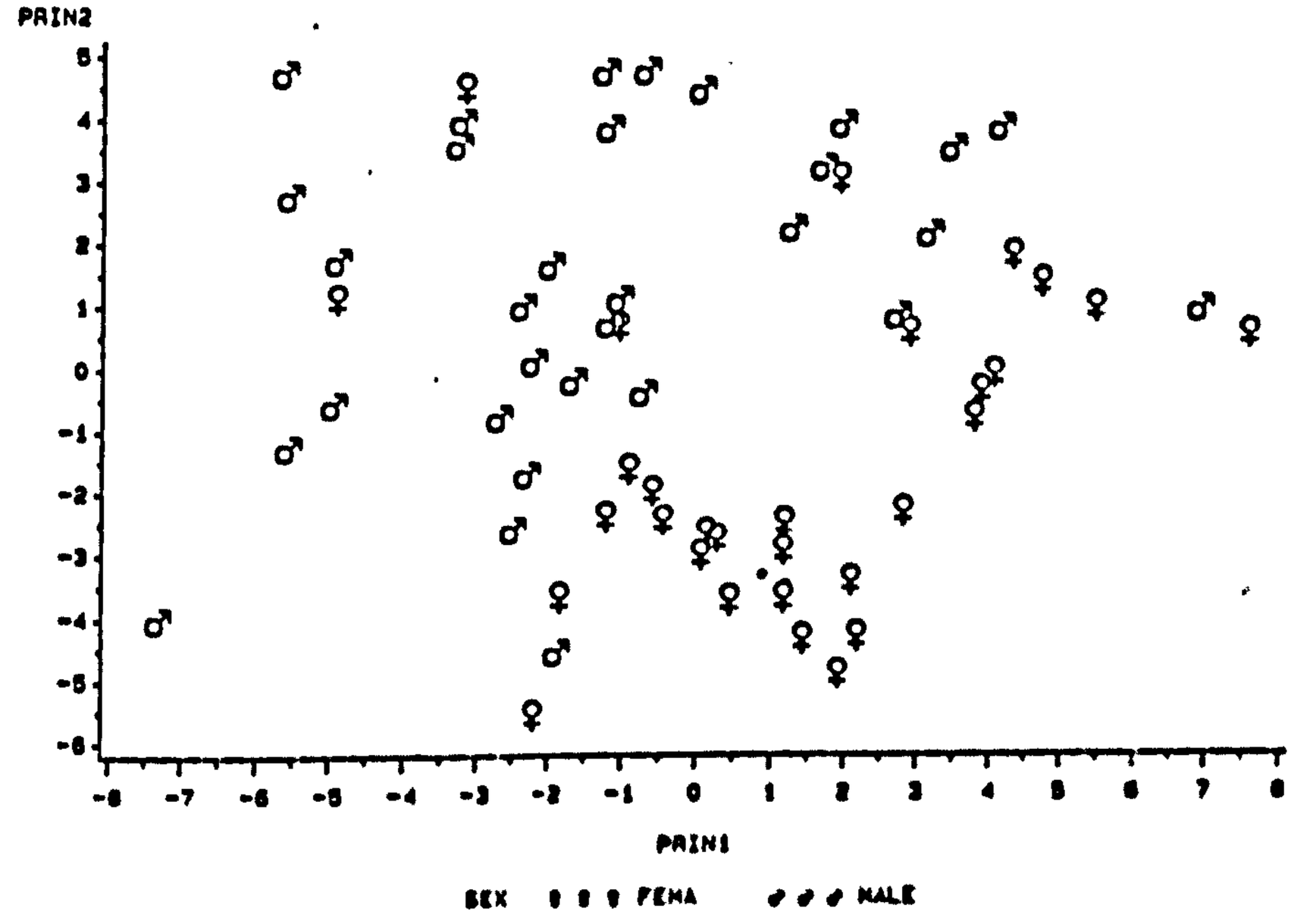
**The correlation of the size variable (square root of area of midline tracing) with the scores of individuals on PC no:**

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| *Gorilla* | −0.26$^{\bullet}$ | 0.54$^{\bullet\bullet}$ | −0.10 | 0.45$^{\bullet\bullet}$ | −0.13 |
| *Pongo* | 0.36$^{\bullet\bullet}$ | 0.41$^{\bullet\bullet}$ | 0.10 | 0.28$^{\bullet}$ | −0.14 |
| *Pan* | −0.07 | −0.05 | 0.10 | 0.29$^{\bullet}$ | 0.33$^{\bullet\bullet}$ |
| *Homo:* | | | | | |
| Cauc. | 0.03 | 0.12 | 0.11 | −0.08 | −0.25 |
| Mon. | 0.28 | −0.03 | −0.17 | −0.30 | −0.30 |
| Neg. | 0.25 | 0.00 | 0.39$^{\bullet}$ | 0.01 | 0.33 |
| Aust. | −0.17 | 0.37$^{\bullet}$ | 0.20 | 0.07 | −0.39$^{\bullet}$ |

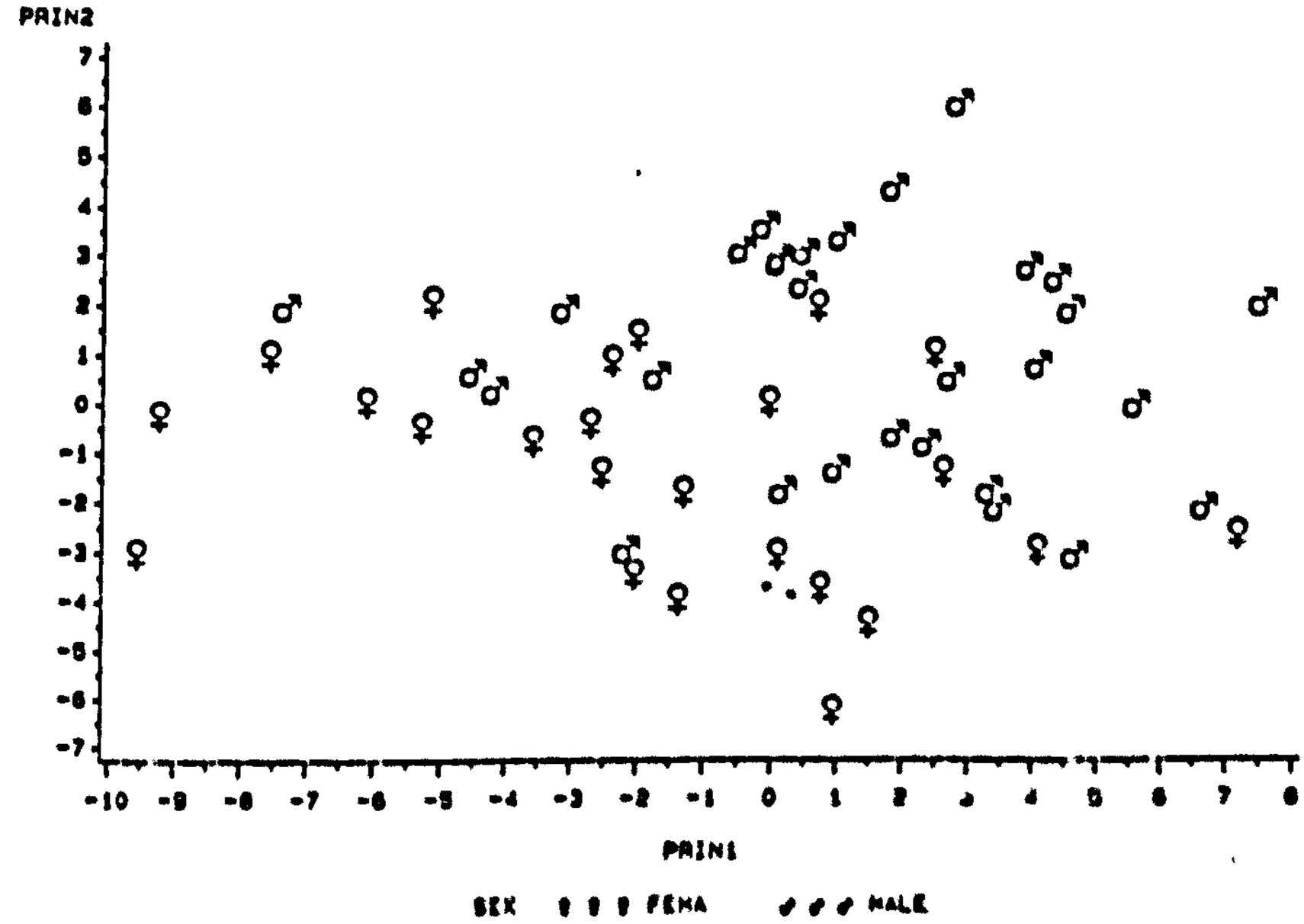
$P < 0.01$ = $^{\bullet\bullet}$

$P < 0.05$ = $^{\bullet}$

FIGURE 3.17 – Principal Components Analysis of 20 scaled sine/cosine Fourier coefficient pairs



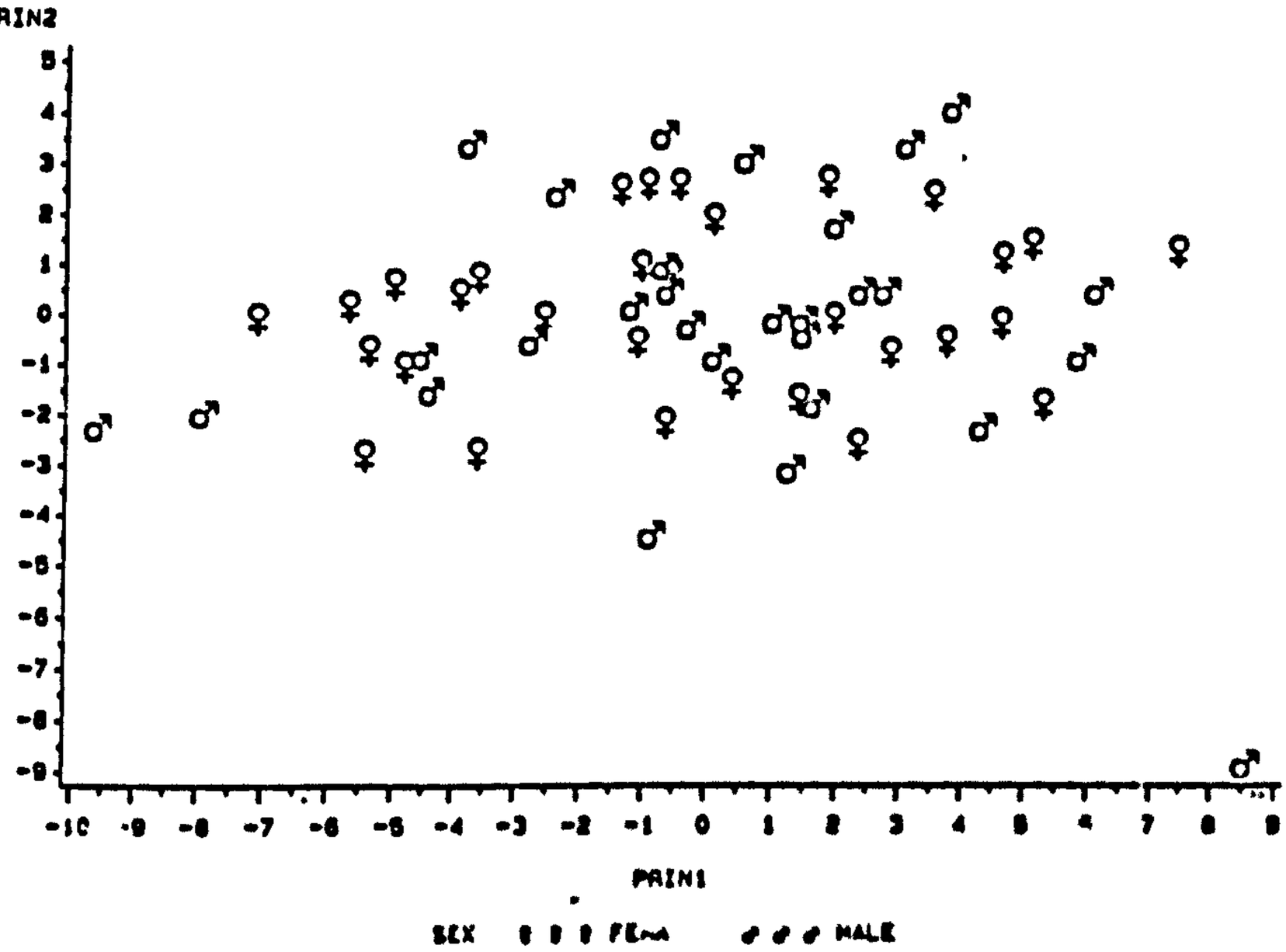

a. *Gorilla*




b. *Pongo*

Fig 3.17

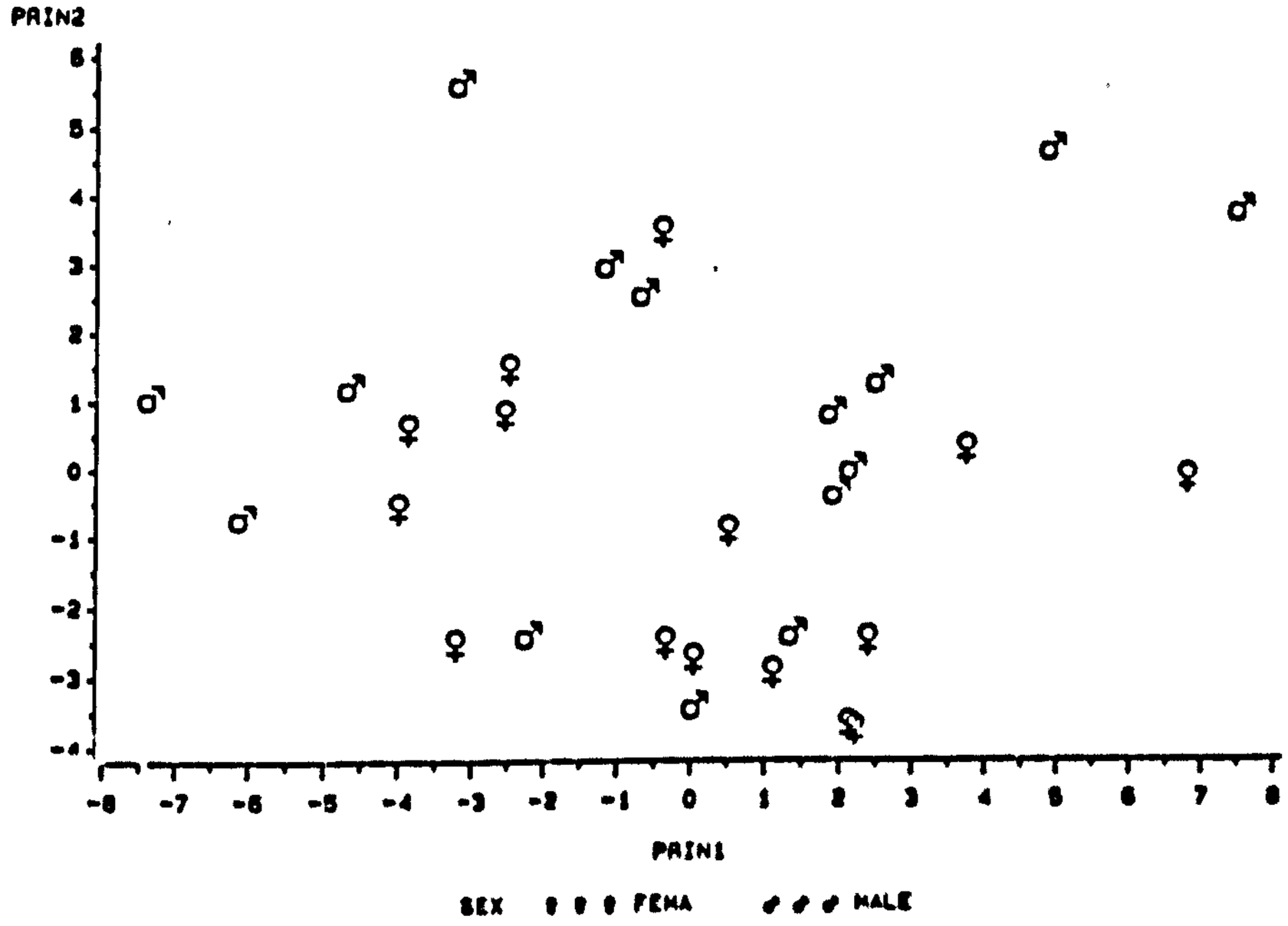
FIGURE 3.18 – Principal Components Analysis of 20 scaled sine/cosine Fourier coefficient pairs



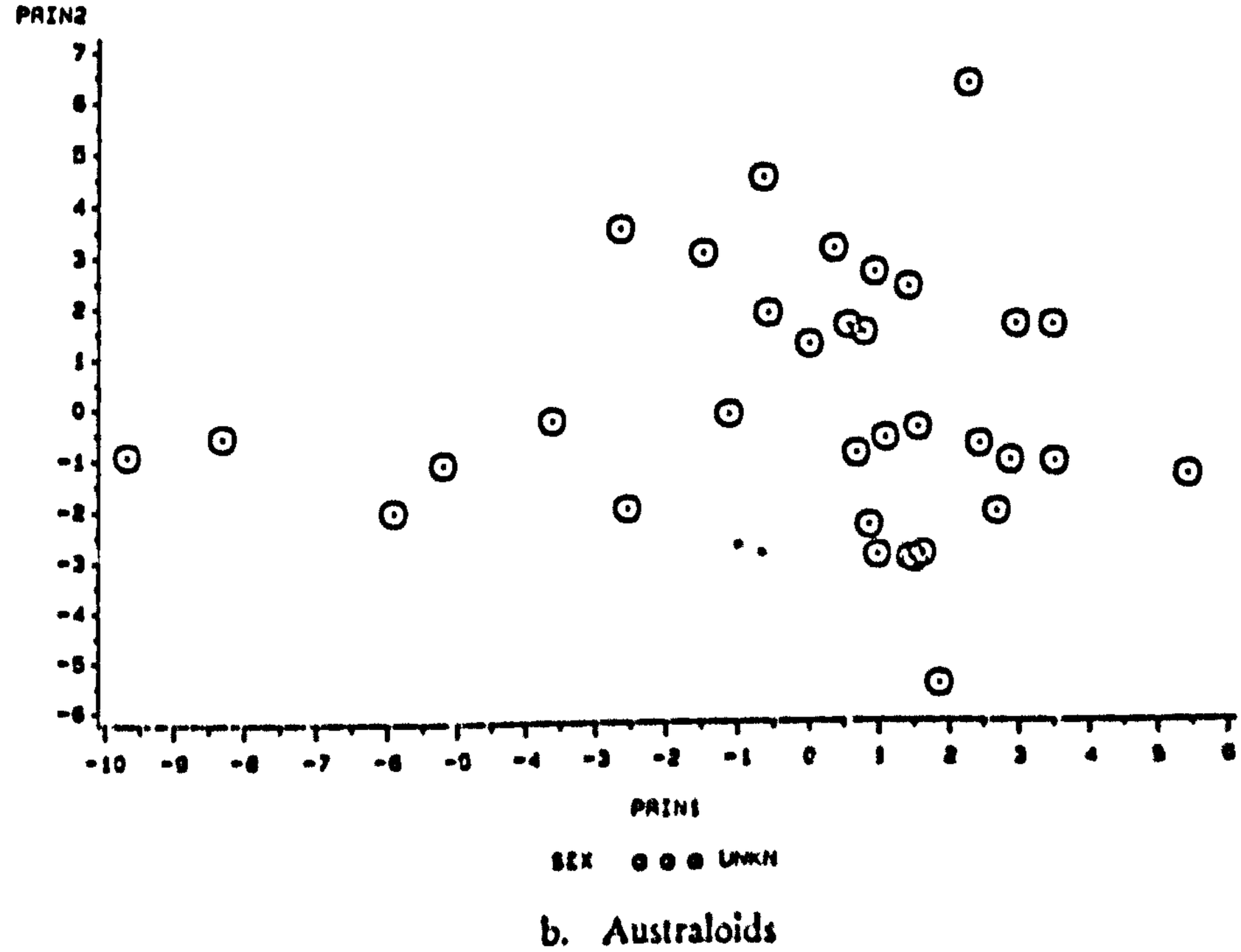

*Pan*

Fig 3.18

FIGURE 3.19 – Principal Components Analysis of 20 scaled sine/cosine Fourier coefficient pairs



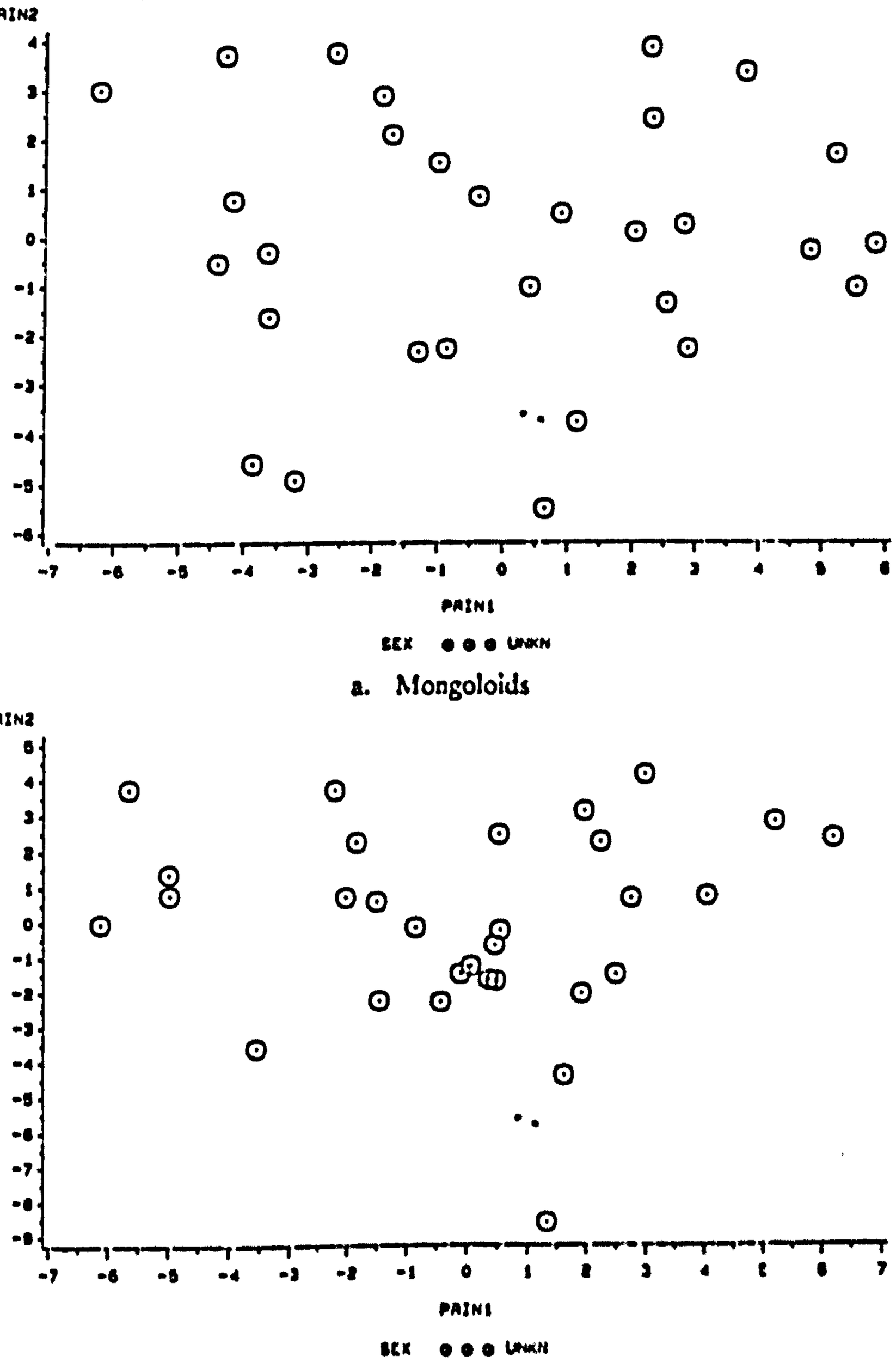

a. Caucasoids




b. Australoids

Fig 3.19

FIGURE 3.20 – Principal Components Analysis of 20 scaled sine/cosine Fourier coefficient pairs




a. Mongoloids




b. Negroids

Fig 3.20

on the early PCs (I and II) is more complex. The results of table 3.16 indicate that there are a number of significant correlations between the scores of individuals on higher PCs and the size variable. This contrasts with the results of the analysis of scaled linear and angular measurements (table 3.14).

This difference in result implies that in the analyses of scaled Fourier data non-size related sources of variation are proportionately more important than in studies of scaled linear and angular dimensions. The fact that there is a greater number of significant correlations of the size variable with the scores of individuals on higher PCs implies, however, that the Fourier data are still describing those aspects of size related shape difference which are influencing the linear and angular measurements.

These differences between the analyses may relate to the fact that Fourier data provide a description of cranial morphology which gives equal weight to all outline points whereas linear dimensions provide a description which emphasises those regions where landmarks are plentiful. The completeness of the Fourier description means that each Fourier component reflects total morphology, including size related effects. These effects have a more diffuse influence in the PCAs and, because each region is sampled according to its contribution to the cranial outline, aspects of shape which are relatively poorly described by linear dimensions and angles have a proportionately greater weighting.

## Patterns of between group variability

The univariate and multivariate studies have indicated that size dimorphism is a significant component of sexual dimorphism in the sexed groups included within this study. The studies also agree that in those groups where sexual size dimorphism is large there is a considerable component of shape dimorphism. Where size dimorphism is small other sources of variability make the detection of concomitant shape dimorphism difficult.

The results presented in table 3.17 go some way to emphasising this finding. The mean size (square root of midline area) of each sexed group together with absolute and relative sexual size differences are listed. The column headed "raw distance" gives values of between-group distances calculated from unadjusted linear and angular dimensions (the set of 25 midline and projected midline linear and angular dimensions). It is clear that these are correlated with sexual size differences. When the data are scaled the between-sex differences are smaller in proportion to the original sexual size difference.

It can be concluded that, in this study, shape differences between the sexes are related to size differences. The univariate and multivariate studies have indicated, however, that the relationship between size and shape difference may vary between genera, species and races. The degree of such variability was further investigated by a series of canonical and discriminant analyses.

## TABLE 3.17

The relationship of shape dimorphism to size dimorphism

Size variable = square root of mid-sagittal area

| GROUP | Mean Size | Size diff. | m/f Size ratio | Raw dist. | Scaled dist. |
|---|---|---|---|---|---|
| *Gorilla* f.<br>*Gorilla* m. | 11.87<br>13.63 | 1.76 | 1.48 | 6.67 | 5.51 |
| *Pan* f.<br>*Pan* m. | 10.22<br>10.54 | 0.32 | 1.03 | 1.96 | 1.73 |
| *Pongo* f.<br>*Pongo* m. | 10.16<br>11.55 | 1.39 | 1.14 | 6.07 | 4.8 |
| Caucasoid f.<br>Caucasoid m. | 14.17<br>14.77 | 0.6 | 1.04 | 2.65 | 2.32 |

Units:

Size = cm.
distances = SDU (Mahalanobis')

Between-group variability - Apes and men

Two canonical analyses were carried out in order to compare the directions of sexual dimorphisms within the sexed groups. The first is an analysis of the first 20 pairs of raw sine-cosine Fourier coefficients (see figure 3.21) and the second is an analysis of the 47 linear dimensions (table 2.3, see figure 3.22).

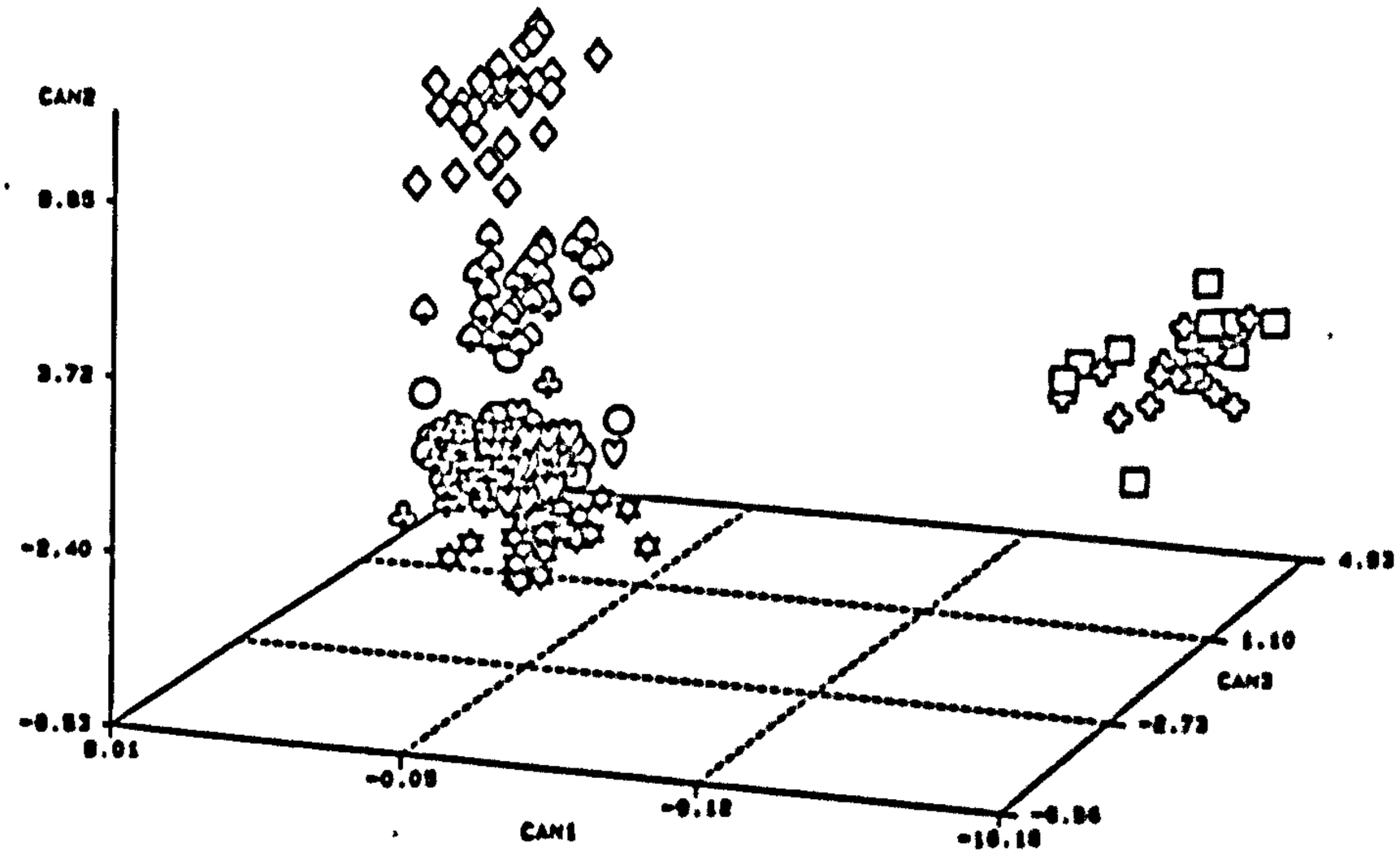
The general pattern of group dispositions in both analyses is very similar to that in the minimum spanning trees presented in chapter 2 (compare figs. 2.20-2.22, with figs. 3.21 and 3.22). The apes form a U shaped grouping with *Pan* at the base of the U, the sexes of *Pongo* make one limb and those of *Gorilla* the other. The caucasoids are distant from the apes.

The plot of the first 3 canonical axes calculated from the Fourier coefficients is given in figure 3.21. The angles between the axes connecting the centroids of the sexes within each genus differ. Shape dimorphism in *Pongo* is mainly revealed by axes 1 and 3, that in *Gorilla* by axes 1, 2 and 3 and that in *Pan* and the caucasoids by axis 3.

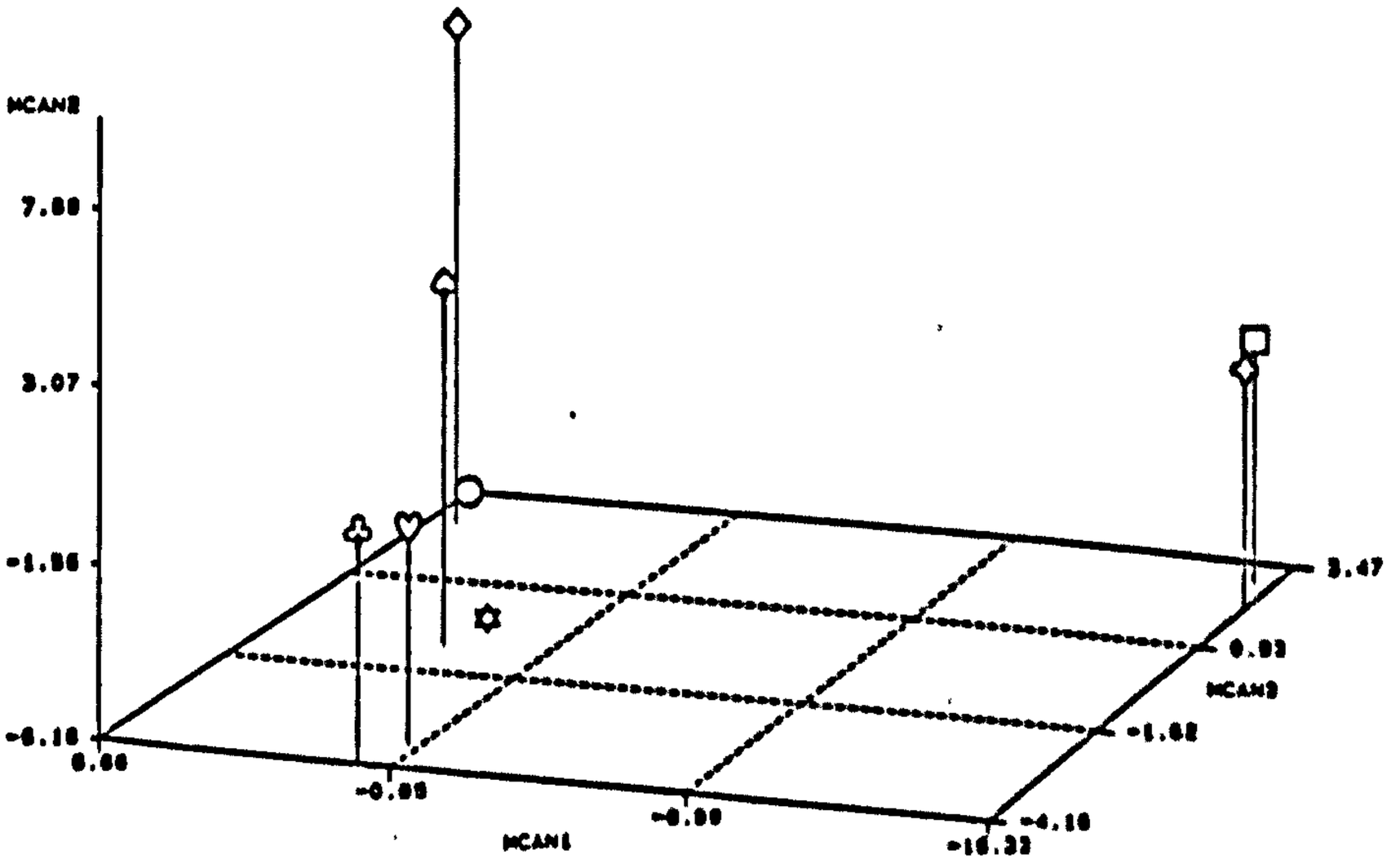
In the analysis of raw linear dimensions (fig 3.22) the variability in axes between the sexes is once again marked. No two taxa have parallel axes. This is entirely consistent with the observation made in the earlier parts of this study that variability characterises vectors of sexual dimorphism within the hominoids.

The principal component analyses of *Pan* and caucasoids have demonstrated that the sexes in these groups cannot be easily distinguished therefore the axes which these analyses reveal are subject to a considerable error. The most clear difference is that between the *Gorilla* dimorphism and the *Pongo* dimorphism.

FIGURE 3.21 – Canonical Analysis of 20 raw sine/cosine Fourier coefficients




a Individuals




b group means

Proportion of total variance accounted for by first 3 axes = 95%

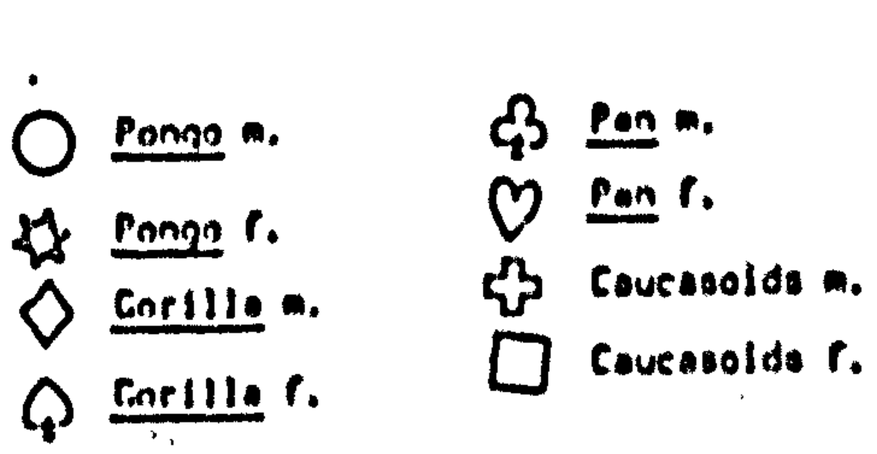
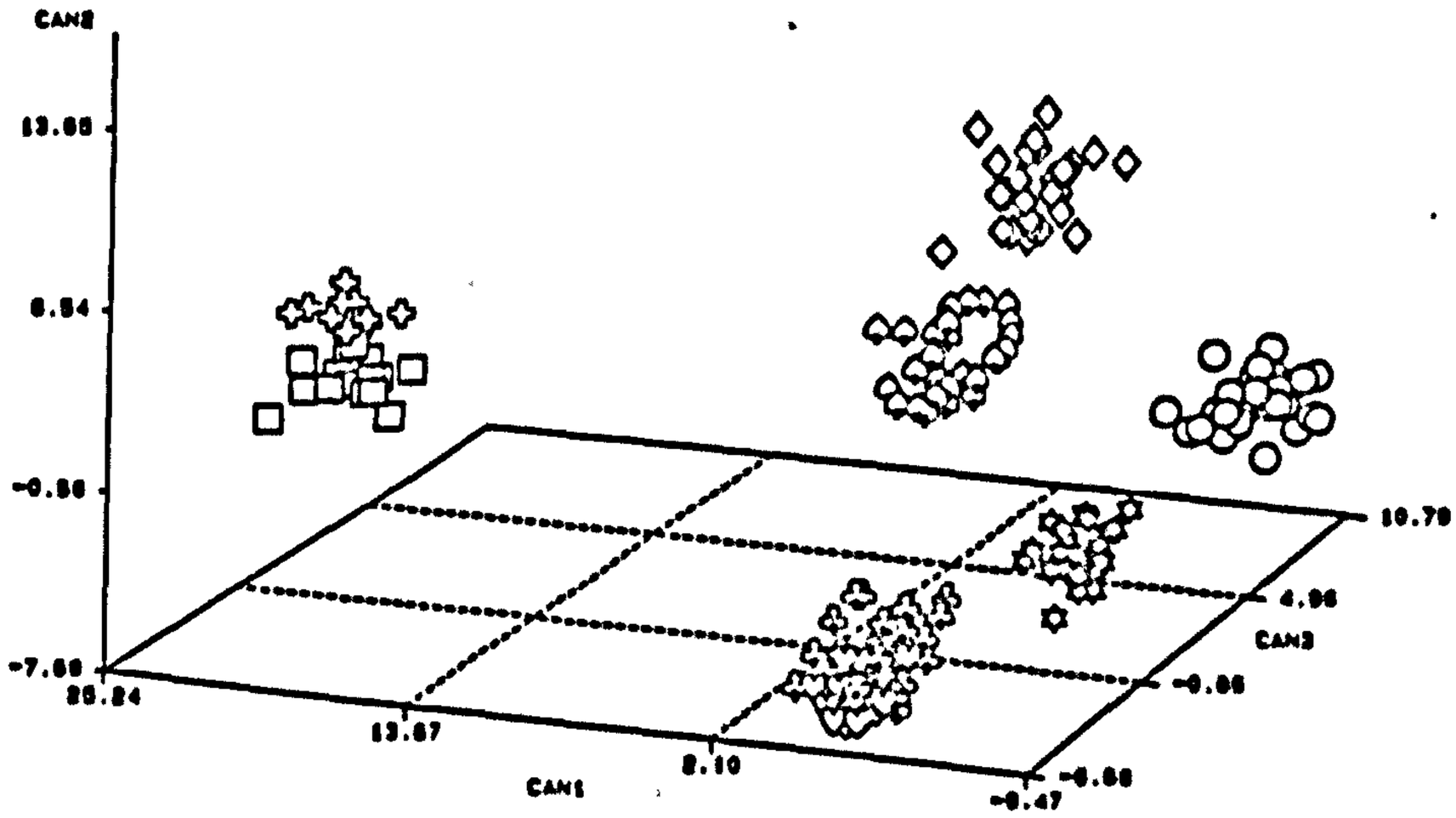
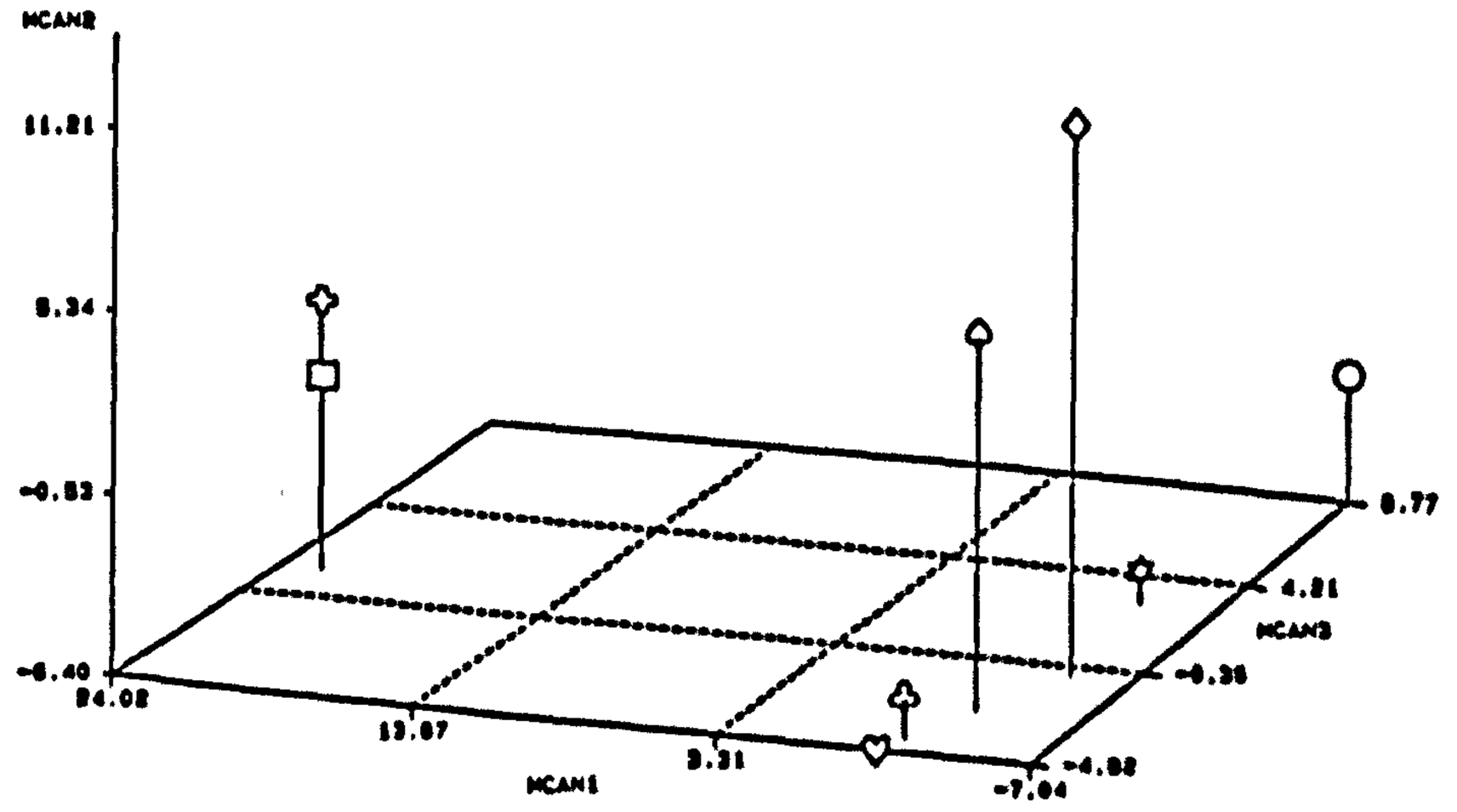



Fig 3.21

FIGURE 3.22 – Canonical Analysis of 47 raw cranial dimensions




a Individuals




b group means

Proportion of total variance accounted for by first 3 axes = 96%

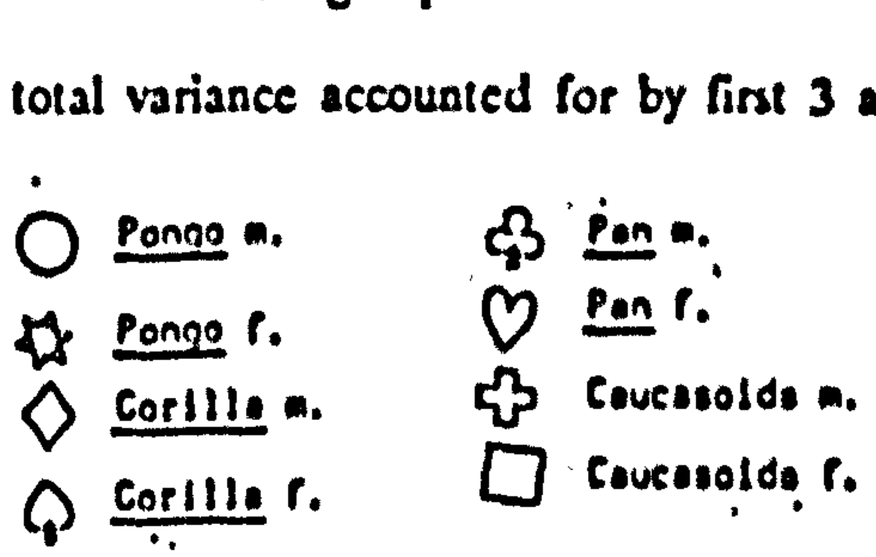



Fig 3.22

## Between-group variability - Men

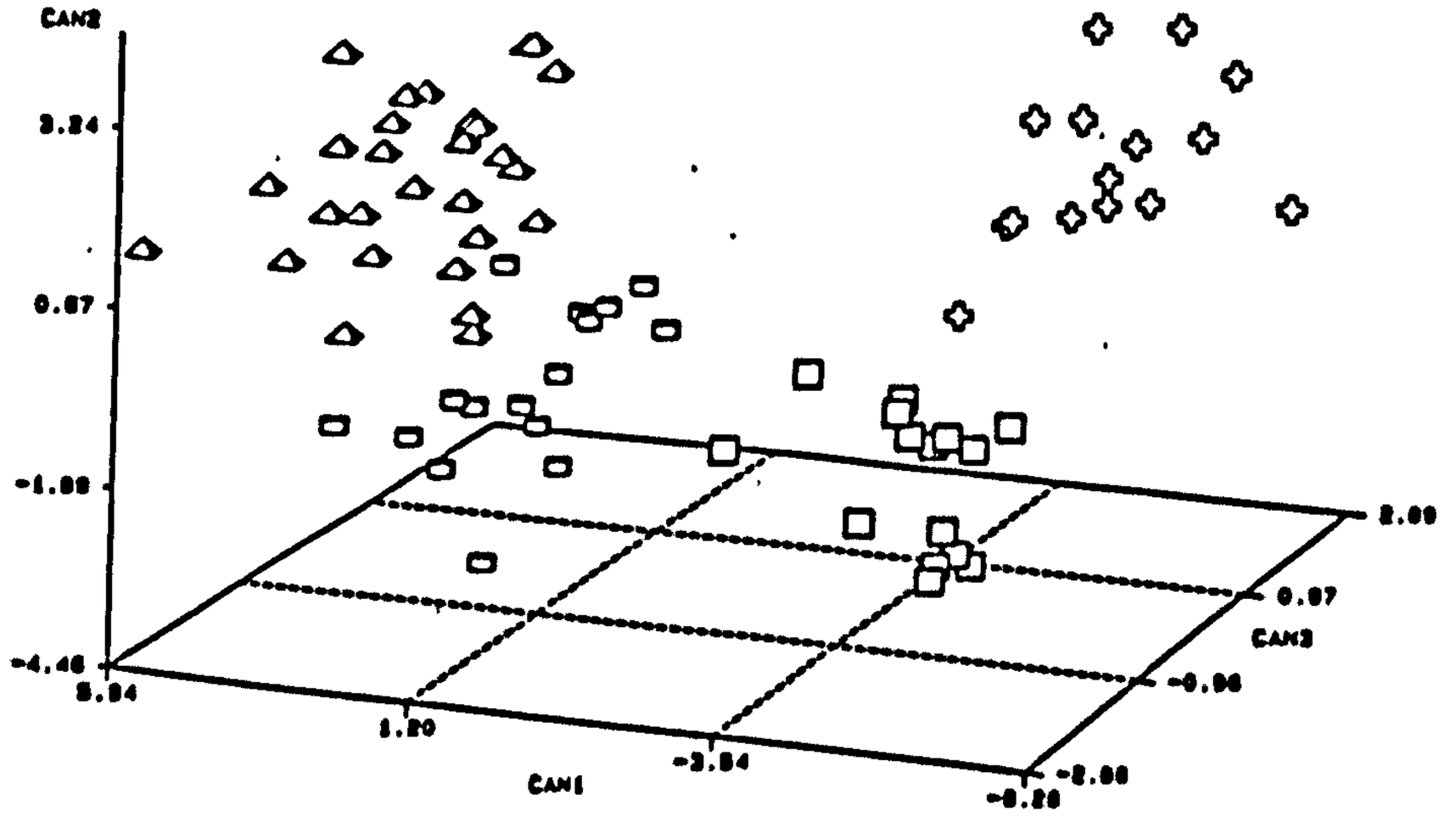
The studies described in the earlier part of this chapter have indicated that variability in dimorphism is not just confined to the between-species level but that there are also variations between the races of man.

Variability between the human races in the pattern of sexual dimorphism was further investigated in a limited study using those cranial dimensions and angles (table 3.1) which were available in the caucasoid sample and in a sample of Hong Kong Chinese crania (both of known sex).

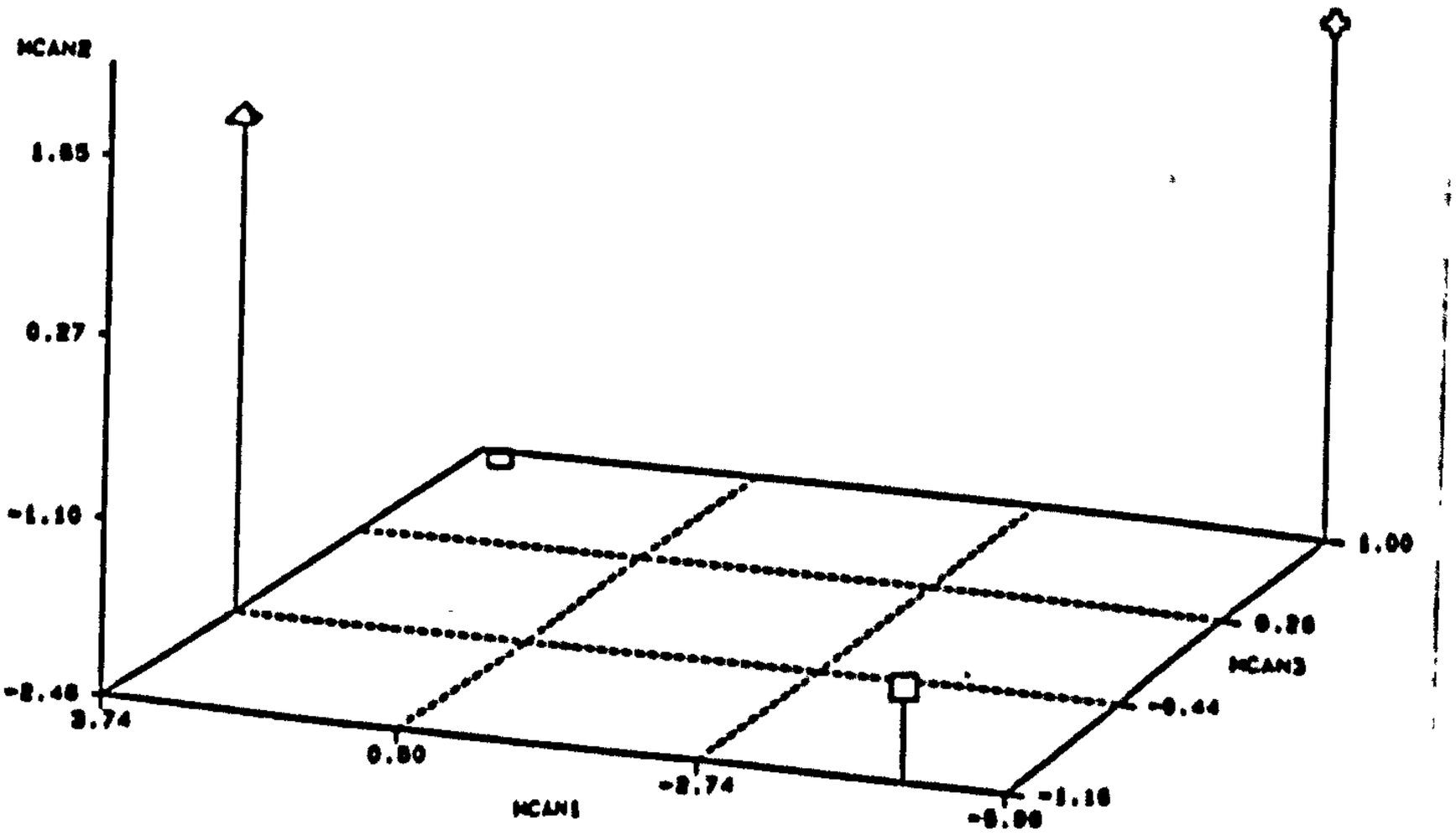
The canonical axis plots from this analysis are presented in figure 3.23. In the plot of group means (figure 3.23b) canonical axis I differentiates caucasoids from mongoloids. The second axis differentiates males from females. On the third axis male caucasoids and female mongoloids are at the positive extreme whilst female caucasoids and male mongoloids have negative scores. Consequently the axes of dimorphism in these two racial groups have a component which is mutually orthogonal. It should be noted, however, that the scales of each axis differ and that the range of the third axis, which demonstrates this difference, is 2 SDU as compared to nearly 10 SDU for the first and 4 SDU for the second.

The canonical analysis suggests that there are differences in the patterns of sexual dimorphism which characterise these two racial groups. This finding is reinforced by the results of a stepwise discriminant analysis undertaken using the variables which were common to the caucasoid and the Hong Kong Chinese cranial samples. Table 3.18 lists, in order, those variables which were found to

FIGURE 3.23 – Canonical Analysis of 31 cranial dimensions from English and Hong Kong Chinese populations




a Individuals




b group means

Proportion of total variance accounted for by first 3 axes = 100%

Caucasoids m.

Caucasoids f.

Mongoloids m.

Mongoloids f.

Fig 3.23

TABLE 3.18

The variables which give the best differentiation between sexes.

| Caucasoids | Hong Kong Chinese |
|---|---|
| Bizygomatic breadth | Angle Opis – basion – nasion |
| Maximum length | Maximum length |
| Nasal breadth | Foraminal length |
| Subnasal height | Foraminal breadth |
| Palatal length | Subnasal height |
| Angle Opis – basion – nasion | Occipital chord |

be most useful in determining the sex of crania belonging to each group. The lists have some variables in common but the relative effectiveness of these variables differs (different order). Some of the variables are well correlated with size (compare with table 3.4) whilst others, e.g. subnasal height, nasal breadth are not. The differences between the lists suggest a difference in shape and size dimorphism between the groups.

# DISCUSSION

The principal aim of this second study has been to further compare Fourier data and linear and angular measurements with respect to their utility in describing patterns of primate cranial variability. The study has concentrated on a comparison of the patterns of cranial variability revealed in modern hominoid groups using both types of data. The discussion is best considered in two parts:

## 1. Patterns of within-group cranial variation

In the introduction to this chapter it was noted that a major component of intraspecific variation in hominoids is attributable to the phenomenon of sexual dimorphism. The studies of previous workers have indicated that, within these groups, differences in size and in shape consequent upon size differences form a considerable source of intraspecific variation (e.g. Wood, 1976, Schmid and Statil, 1984, Clutton-Brock, 1985, Leutenegger and Cheverud, 1985, and Oxnard, 1987).

One hypothesis that this study has set out to test is that cranial sexual dimorphism is related to sexual size differences in the hominoids.

The univariate studies of both the Fourier data and the linear measurements have shown that dimorphisms in means are generally significant in those variables which are significantly correlated with the size variable. In contrast, dimorphisms in variances are present in a considerable proportion of variables which are not significantly correlated with the size variable.

The results of the principal component analyses indicate that, within the studied groups, size and sexual shape differences are inextricably connected. Those principal components which order crania by sex are also those which have a significant correlation with the size variable. They account together for a considerable proportion (though never more than half) of the total within-group variability. When the data are scaled crania are still ordered by sex along certain principal components in certain groups and the scores of crania on these components also correlate significantly with size. These studies suggest that sexual dimorphism includes an element of shape dimorphism and that all of the observed shape dimorphisms are size related. Dimorphisms of variance are, however, more independent of size dimorphism.

These findings broadly agree with those of Oxnard (1987) who investigated the relationship of size differences and sexual dimorphism within a wider range of primate groups. He found, however, that in some taxa, e.g. *Galago*, the degree of sexual shape dimorphism is large despite a small size difference – "this finding suggests that there may be major sexual dimorphisms in overall body proportions that are scarcely related to size at all. It would obviously be false to claim that size is not implicated in at least a part of the sexual dimorphisms ..... but the data clearly demonstrate that there must be many other parts of the sexual dimorphisms that are associated with other factors" (Oxnard, 1987: p32).

A further hypothesis which has been tested in this study is that the hominoid taxa share a common pattern of cranial sexual dimorphism.

The evidence of the univariate study is that the patterns of dimorphism within hominoids do vary. Variations have been noted in the number and types of variables which have significantly different means and variances between sexes. The multivariate studies have indicated that further variations exist between taxa in the proportion of total within-group variation which is related to size and sexual shape differences. There are even considerable differences between the racial groups of Mankind. The consequence is that, in different races, different variables have different relative weightings in discriminant functions which are designed to classify crania by sex.

The finding of variability in patterns of sexual dimorphism within closely related groups is a common one. The work of Albrecht (1978b) on the craniofacial morphology of the Sulawesi macaques shows some species differences in the directions of the male-female axes in canonical space (p59. fig.16). The study of Creel and Preuschoft (1984) also demonstrates considerable differences in the vectors of sexual dimorphism in the crania of different gibbon species (p594, fig. 44.8) (though none of these workers place much emphasis on these differences).

Despite this it appears that the variability of shape dimorphisms seen between the races of man is relatively small and that sexual size differences (including common allometric shape differences) will provide a broadly adequate basis for the sex diagnosis of crania. This concurs with the findings of Calcagno (1981) and Uytterschaut (1986) which were reviewed earlier.

In summary, the findings of this study indicate that a major source of variation within the hominoids is size and its consequences. These size related

phenomena include, at least within the groups under study, a considerable component related to sexual shape dimorphism. The relationship between sexual shape dimorphism and size dimorphism is not simple, the same size difference between sexes may be associated with shape differences which vary even between closely related groups.

## 2. Comparison of Fourier data and linear and angular measurements

From the studies presented in the first chapter it appears that in studies of the crania of extant hominoids these two types of data result in broadly similar patterns of between group relationships and allow approximately the same degree of accuracy in identifying crania by specific and racial group.

The principal aim of this study has been to test the hypothesis that sine–cosine Fourier data and linear and angular measurements provide similar results in studies of within–group variability.

In the univariate studies presented in this chapter both the Fourier data and the linear dimensions indicate that the crania of caucasoids and *Pan* show fewer sexual differences in means than *Pongo* and *Gorilla*. In both sets of data those variables which show a sexual size difference in a particular group are, in general, significantly correlated with the size variable. A further point of agreement is that both sets indicate marked differences between the racial groups of *Homo* in the numbers, magnitudes and patterns of significant correlations with the size variable.

The Fourier data and the linear dimensions both indicate that different patterns of dimorphism of variances characterise different groups. The types of

data disagree, however, in that the linear dimensions indicate that *Pongo* and *Pan* have a similar number of dimorphisms of variances whilst the Fourier data indicate that *Pan* and *Gorilla* have a similar number.

The contrasts are more marked in the principal component analyses. In the PCAs of raw linear and angular measurements sexual differences are only demonstrated along the first principal component and the scores of crania on this component correlate markedly with the size variable. In contrast, the PCAs of raw Fourier components do not exclusively show sexual differences on the first component. These differences are more widely spread over several components and the size variable correlates significantly, but to a lesser extent, with the scores of crania on several higher order components.

The differences between the results derived from scaled Fourier components and those from scaled linear and angular measurements are similar to those observed in the studies of raw data. There is a lesser degree of sexual separation observed on the first two PCs and the size variable correlates significantly with the scores of crania on more of the higher order PCs in the analyses of Fourier data.

In the principal components analyses of Fourier data sources of variation which are not size related are proportionately more important than in PCAs of linear and angular measurements.

This difference is attributable to fundamental differences between the data. Fourier data are less size dependent when the first cosine term is ignored (cosine 0 is effectively a size variable) and they provide a more complete description of cranial morphology. The Fourier data give equal weight to all outline points and as such describe those regions where there are few landmarks

with as much fidelity as those where landmarks are more plentiful. The consequence is that more aspects of cranial variation are described and that size related effects are proportionately less prominent.

It is concluded, therefore, that the analyses of sine–cosine Fourier coefficients have lead to broadly similar findings to those obtained from linear and angular dimensions in this study of patterns of within–group variability. The principal differences in result are a consequence of fundamental differences in the data such that variations which are purely size related assume a lesser importance relative to other sources of intra–group variation.

# CHAPTER 4

## Patterns of cranial variation within and between certain groups of fossil hominoids

# I. A STUDY TO ASSESS THE APPLICABILITY OF FOURIER ANALYSIS TO THE STUDY OF THE CRANIAL MORPHOLOGY OF VARIOUS FOSSIL HOMINIDS

## INTRODUCTION

In this chapter I present a study of patterns of cranial variation within and between certain groups of fossil hominids. It builds on the studies of methods of describing cranial form presented in chapter 2, and the examination of the applicability of these methods in studies of cranial variation in extant hominoids in chapter 3.

### Summary of previous chapters

In the earlier chapters I have explored a variety of methods for the description of biological form and have presented a study which compares their abilities to allow an assessment of the phenetic relations of modern crania and to allow the identification of material of unknown provenance. Fourier analysis and linear dimensions and angles performed well on both counts.

A second study examined the relative performance of these two methods in a study of patterns of within group variability. Fourier analysis gave similar results to those obtained from linear dimensions and angles but in PCAs the influence of size related variation was reduced relative to other sources of variation.

Aims of the studies presented in the current chapter

This chapter sets out to further examine the value and utility of Fourier analysis, this time in the study of between group phenetic relations using fossil and extant representatives of the Hominoidea.

The studies presented earlier in this thesis have shown a fair correspondence between the patterns of phenetic relationships which are implied between extant hominoid crania when different methods of description of cranial morphology are employed. This result does not necessarily imply, however, that the same is true when fossil material is studied.

The study of fossil hominid material presents several problems. The first is that there is considerable debate about the exact limits of biological species, the definition of acceptable taxa being based upon expert appraisal and phenetic criteria. Second, a considerable proportion of the available material is badly fragmented, incomplete, and reconstructed. A third problem arises from the wide geographical distribution of the original material. As a result the cost and time required to examine it all is prohibitive for an exploratory study of the present type.

The first problem, that of the delineation of acceptable species limits, is not intractable. Taxa can be defined by the discovery of morphological discontinuities in the fossil record (see Simpson, 1961, Sneath and Sokal, 1973) provided that adequate estimates can be made of missing or damaged regions

of the crania. The second problem is more difficult. The reconstruction of missing parts and the estimation of dimensions from missing regions is by nature a subjective exercise. For the most part the data used in this study have been taken from casts of reconstructions made by a number of authoritative workers in the field and where estimates have been made they are based upon the experience of two senior anatomists and have been checked by myself (see Appendix A). The third problem, that of using casts, is addressed later in this in this study.

It is a primary purpose of this study to further examine the degree of correspondence in the patterns of phenetic relationships between hominid crania which are demonstrated when angles and dimensions and Fourier data are compounded in phenetic analyses. If analyses of Fourier data show a high degree of correspondence with analyses of the more traditional data then the study of cranial morphology (in a strictly phenetic sense) may be greatly simplified because Fourier data can be collected automatically (see O'Higgins and Williams, 1987). To date, however, no single study exists in which Fourier analysis and a number of other, "new", methods for the description of the complex morphology of biological structures have been compared with the more traditional techniques.

The current study aims, therefore, to provide comparative data on two different approaches to the description of morphology. It tests the hypothesis, implied by the results of the study of chapter 2, that the pattern of between

group phenetic relationships derived from Fourier data is consistently very similar to that derived from a series of cranial dimensions taken from the same anatomical parts.

It has already been pointed out in the earlier chapters of this thesis that linear and angular measurements have to be taken between fixed landmarks and that there is a scarcity of suitable landmarks in certain parts of crania (e.g. the vault), relative to others (e.g. the base). With this in mind some difference in phenetic relationships is to be expected when the different data are compounded. This study further aims, therefore, to examine any such differences and to consider the utility of Fourier analysis in the context of any such discrepancies.

Considering the fact that the studies presented here utilise casts of the crania of a number of fossil hominids it has become a secondary aim to provide confirmation or otherwise of the patterns of phenetic relationships implied by the studies of previous workers. To this end, a review of such previous studies is presented and the discussion compares and contrasts the results of the current studies with those from previous ones.

Summary of the current chapter

This chapter begins with a brief review of the hominid fossil record which is presented to set the scene for this final study so that the newcomer to studies of fossil hominids can be made aware of the context of this work. The study proper is preceded by a review of published multivariate studies of fossil and extant hominoid crania. There follows a description of the materials and methods

which were employed and this is in turn followed by a description of the results. The discussion concentrates on the three aspects discussed above: the degree of agreement between the studies of Fourier data and more conventional data, the sources of any observed differences and a comparison of the results of the current studies with those of previous workers. In addition to this a consideration of the phenetic validity of the OTUs selected for this study is presented in Appendix B.

## II. MAN AND HIS FOSSIL RELATIONS

When Charles Darwin published "On the Origin of Species" in 1859 only a few fossils bearing upon the evolution of man were known (though their significance had not yet been appreciated). One was found at Forbes' quarry, Gibraltar in 1848 (Busk, 1865) and the other in the Neander valley, Germany in 1856 (Fuhlrott and Schaaffhausen, 1857). They later came to be known as examples of Neanderthal man. Since this time a variety of other fossil hominids have been unearthed. Excluding representatives of *Homo sapiens* they have been found in various regions from the southern tip of Africa to Indonesia. The fossils occupy a time span ranging from 5 million years ago to almost the present day.

By far the most fruitful sites are those associated with the great rift valley of East Africa where fossiliferous beds in Ethiopia, Kenya and Tanzania have yielded specimens attributed to *Australopithecus* and *Homo*. From South Africa specimens have been discovered which are attributed to *Australopithecus africanus*, *Australopithecus robustus* and *Homo*.

From the Far East, Middle East, China and Java, specimens attributed to *Homo* are known. From Europe and parts of Africa a variety of relatively recent specimens of *Homo* have been found. These comprise archaic representatives of *Homo sapiens*, the Neanderthals, and *Homo sapiens* of modern aspect from the Upper Paleolithic.

In total a large number of cranial and post cranial remains have been discovered. They seem to span the evolutionary spectrum of mankind from a

time close to the divergence of hominids from the African apes.

In this chapter I shall review the evidence for the evolution of *Homo* paying particular attention to what is known of the cranial morphology of extinct types. The morphology of the dentition, mandible and any known post cranial material is not discussed in any detail, however, since none of this material is included in the studies described later in this chapter. It seems reasonable to take the specimens in chronological order, starting with the Australopithecinae.

# THE AUSTRALOPITHECINAE

## A. Morphology and Provenance

### South African Australopithecines

The first fossil australopithecine to come to light was the immature cranium discovered in 1924, at Taung in South Africa (Dart, 1925). Since this first find the sample of known australopithecines has been considerably enlarged (see Oakley *et al.*, 1977, Howell, 1978, Johanson, White & Coppens, 1978). Exploration in South Africa has yielded material from several sites, Sterkfontein, Kromdraai, Swartkrans and Makapansgat and at least two South African australopithecine species have been discerned viz. *Australopithecus africanus* and *Australopithecus robustus* (though some authorities consider that there is evidence for three or more species, see Grine, 1981, Howell, 1978 and below)

*Gracile material*

Later australopithecine finds include an adult cranium from Sterkfontein (Broom, 1947). Initial descriptions attributed this skull, Sts 5, to *Plesianthropus* though nowadays it has been sunk, together with all similar, gracile, material into *Australopithecus africanus* (see Howell, 1978, Johanson and White, 1979, Grine 1981). Robinson (1967, 1972) has argued forcefully for the inclusion of this group in *Homo* and has suggested that the correct nomen should be *Homo africanus*.

Since this first discovery the Sterkfontein site has yielded a number of cranial and postcranial remains (see Oakley *et al.*, 1977). Most of this material has been attributed to *Australopithecus africanus* though there has been a suggestion that a skull, StW53, which seems to come from more recent deposits may be a representative of *Homo habilis* (Hughes and Tobias, 1977 and see below).

More specimens which are now attributed to *Australopithecus africanus* have been unearthed at Makapansgat (see Oakley *et al.*, 1977). Initial descriptions (Dart, 1948, Broom, 1949) distinguished the first Makapansgat specimens from previously known South African gracile material chiefly on the basis of a presumed larger cranial capacity. A new species *A. prometheus* was named. Robinson (1954) in reviewing the then known South African material considered that the occipital and innominate morphology did not differ significantly from that encountered in the Sterkfontein material. Accordingly, he suggested it be included with the other gracile australopithecine material in a single species and subspecies, *A. africanus transvaalensis*.

*A. africanus cranial morphology*

Specimens attributed to this species exhibit a cranial capacity in the range 425–485 cc. (Holloway,1973). They have a lightly constructed ovoid cranium with a reduced postcranial constriction and a marked parietal curvature relative to the apes. They show minimal or no sagittal cresting and a variably salient transverse occipital torus.

They have a continuous supraorbital torus and the calvarium rises above the upper orbital margin. The position of the nasion is relatively low with respect to living apes. The face is moderately prognathous with a projecting subnasal part of the maxillae. The nasal margin is elevated and bordered inferolaterally by a continuation of the canine pillars. (Rak, 1985)

The cranial base is expanded with a relatively low angle of the petrous axis to the median sagittal plane. The foramen magnum faces inferoposteriorly and the occipital condyles are relatively small and posteriorly placed (Howells, 1973).

*Robust material*

The first discovery attributed to the robust australopithecines was made at Kromdraai in 1938 (Broom, 1938). The find (TM 1517) consisted of a partially complete, heavily built cranium, with considerable postorbital constriction, a large face and a small neurocranium. It was designated the holotype of *"Paranthropus robustus"* (Broom, 1938).

Several more robust cranial and post cranial finds have been unearthed at Swartkrans (Oakley *et al.* 1977). The first find comprised a left mandibular fragment and three upper teeth (SK 2,3,4 and 6). The mandible was designated the holotype of *"Paranthropus crassidens"* (Broom, 1949).

The making of a generic distinction between this "robust" material and the South African "gracile" material and of a specific distinction between the material from Swartkrans and Kromdraai has been a matter of debate (Gregory and Hellman, 1939, Simpson, 1945, Mayr, 1950, Broom, 1950, Robinson, 1954, Brace,

1969, Wolpoff, 1974, Howell, 1978, Grine, 1981, Wood and Chamberlain, 1987) but is now widely accepted (Grine, 1981, Olson, 1985, Dean, 1986).

*South African "Paranthropus" cranial morphology*

The cranial morphology of *"P. crassidens"* is better known than that of *"P. robustus"*, the Kromdraai material being less plentiful and less complete than that from Swartkrans (Oakley *et al.*, 1977, Howell, 1978). Rak (1983) makes no distinction in cranial morphology between the two samples. However, Howell (1978) differentiates them on the basis of "certain discernible and often mensurable characters of the craniofacial skeleton and the deciduous and permanent dentition". Grine (1985) has further examined the dental evidence for a specific distinction and considers that Howell's (1978) conclusion is "most strongly supported by the multitudinous features in which the Kromdraai and Swartkrans australopithecine dentitions differ" (see discussion, later).

Overall the cranium of both samples is more robustly constructed than that of *A. africanus*. The sagittal and nuchal crests are well developed, the vault is thin walled and spheroidal and there is considerable postorbital constriction. Cranial capacity is in the region of 530 cc. (Holloway, 1983). The vault rises only marginally above the upper orbital margin (Howell, 1978).

There is a strongly developed supraorbital torus and a prominent glabella. The face is broad, and generally flat. There is considerable forward projection of the zygomatic elements and the pyriform aperture is set in the resultant midfacial hollow. The maxillae are broad and the infraorbital foramen is set

relatively low (Howell, 1978, Rak, 1983). The subnasal maxilla is prognathous. The lateral part of the inferior margin of the orbit is wide, blunt and extended anteriorly (Rak, 1983). The zygomatic is large and vertically deep with a small anterior and larger lateral facing surface.

The cranial base is relatively shortened, the foramen magnum is relatively long and the petrous temporal is aligned more coronally than that of *A. africanus* (Howell, 1978, Dean and Wood, 1982)

*Dating of South African Australopithecine sites*

The dating of the Sterkfontein remains is somewhat problematical since the deposits are not amenable to radiometric or chemical dating methods (MacDougall and Price, 1974). The gracile australopithecine material from Sterkfontein has all come from deposits (Member 4) tentatively dated at between 2.5 and 3.0 million years b.p on faunal grounds (Cooke, 1970). The putative *Homo habilis* cranium, StW 53, was discovered in deposits (Member 5) dated at 1.85 to 2.0 million years b.p (Delson, 1984 also see Grine 1981, Howell, 1978).

The Taung remains are much less clearly dated, and estimates vary from less than 1.0 to 2.0 million years b.p. (see Grine 1981, Delson, 1985, Tobias, 1978a).

As with other South African sites the Makapansgat site has proved difficult to date and reliance has to be placed on faunal correlations. The australopithecine material has been dated at between 2.5 and 3.0 million years

B.P. by such correlations (Cooke, 1970). Recent paleomagnetic evidence supports a date of greater than 2.9 million years B.P. (McFadden *et al.*, 1979).

The dating of the Kromdraai and Swartkrans sites suffers from similar difficulties. Current best estimates place the Kromdraai hominid bearing layer in the span 1.0 to 2.0 million years b.p. (Vrba, 1981, Partridge, 1982). Vrba (1975) has placed the hominid (Australopithecine) bearing member I of the Swartkrans site at 1.5 −2.0 m.y. B.P. on the basis of faunal correlations.

## East African Australopithecines

### *Robust material*

The first discovery of East African robust australopithecine material was an almost complete cranium, OH 5, which was initially referred to a new genus *Zinjanthropus* and given the species name *boisei* (Leakey, 1959). Subsequently it has been incorporated in *Australopithecus* though the species name has been retained (Tobias, 1967). Since this first discovery of robust australopithecine material in East Africa there has been a steady increase in the number of similarly attributed remains from Olduvai (Oakley *et al.*, 1977), Koobi Fora (the most notable of which in the context of this thesis is the complete cranium KNM−ER 406, Leakey, 1970, Leakey, Mungai, and Walker, 1971, Oakley *et al.*, 1977), Omo, Peninj and Chesowanja.

The fossils from Koobi Fora provide the most comprehensive evidence for *A. boisei*. Although most of the material recovered since KNM−ER 406 (Leakey, 1970) has been referred to *Australopithecus sp. indet.* most workers accept that

a major part represents *A. boisei* (Wood and Chamberlain, 1987).

A variety of fragmentary remains which have been attributed to *Australopithecus boisei* have been recovered from the Shungura formation in the Omo river region, Ethiopia (Howell, 1969, Coppens, 1980, Grine 1981, Wood and Chamberlain, 1987). From Chesowanja two partial crania (Carney *et al.*, 1971, Gowlett *et al.*, 1981) and dental fragments (Bishop *et al.*, 1975) which have been allocated to *A. boisei* have been found (Szalay, 1971, Howell, 1978, Wood and Chamberlain, 1987). From Peninj an adult robust australopithecine mandible has been recovered (Leakey and Leakey, 1964).

A relevant recent discovery is that of a cranium and mandible (WT−17000, WT16005) from the western shore of Lake Turkana (Walker *et al.*, 1986). Recent appraisals of this material have suggested that despite displaying a morphology quite like that of *A. boisei* it differs from the known East African robust australopithecines in displaying a number of more primitive features (Walker, 1987, Leakey and Walker, 1988).

*Cranial morphology of A. boisei*

The cranium of *A. boisei* bears a number of similarities to the South African robust australopithecines in being heavily constructed − especially in the facial region − having a small spheroidal braincase, a cranial capacity in the region of 510−530 cc (Holloway, 1983), marked postorbital constriction, and prominent muscular ridges.

It differs (Rak, 1983) from the South African sample of robust australopithecines, however, in having a less complex topography of the facial mask which is reflected in a smoother and visor-like infraorbital region. Rak (1983) also contrasts the facial morphology of *A. boisei* with that of the South African robust australopithecines in having more lateral flaring of the zygomatic arches, no maxillary fossula, a relatively sharp infraorbital rim, a more massive interorbital region, and a marked prenasal fossa (Tobias, 1967). The presumed male specimens have very large facial heights with respect to their bi-orbital breadths.

Further clear differences from the South African "robusts" are manifest in the dental proportions, with massive postcanine teeth (Tobias, 1967, Howell, 1978). Grine (1985) has also indicated that the deciduous dentition morphology serves to differentiate East from South African robust material.

*Dating of East African robust australopithecine sites*

The Olduvai robust australopithecine material was found in upper Bed I and lower Bed II which suggests a date of about 1.7-1.8 million years b.p (Hay, 1976). At Koobi Fora the cranium KNM-ER 406 was found below deposits dated at approximately 1.65 million years b.p. and above deposits dated 1.9 million years b.p. (McDougall, 1985, McDougall *et al.*, 1985). The older members of the Omo site are dated at about 3.3 million years b.p., and the younger at 1.4 million years b.p (Brown, McDougall, *et al.*, 1985b) though the robust fossils at Omo are not known from the early levels. The Chesowanja

australopithecine site has been given a minimum age of 1.34 m.y. B.P. (Bishop *et al.*, 1975). The cranium and mandible found separately to the west of Lake Turkana (WT17000, WT16005) have been dated at approximately 2.5 m.y. B.P. (Walker *et al.*, 1986).

*East African gracile material*

A considerable number of remains of gracile australopithecines have come from Laetoli, Tanzania, (Leakey, M.D., *et al.*, 1976, White, 1977, White, 1980). They consist, for the most part, of isolated teeth and mandibular fragments. Initial assessments placed the material within the genus *Homo*, no specific name being given.

A more extensive series of hominid fossils comes from Hadar in Ethiopia. The finds include a partial skeleton (AL 288–1) of a small individual, presumed female because of its size and pelvic morphology, some femoral and cranial fragments and a remarkable collection of remains from at least 13 individuals who are believed to have died together in some natural catastrophe (the sample is described by Johanson and co–workers in a series of papers in the American Journal of Physical Anthropology, 57:4 1982).

Initial accounts of these finds affined the then known material to *Australopithecus* and *Homo* (Johanson and Taieb, 1976). Following the discovery of more material, and further study, a new taxon, *Australopithecus afarensis*, was created. All of the Hadar hominids were placed within this species together with the similar material from Laetoli (Johanson, White, and Coppens, 1978,

White, Johanson, and Kimbel, 1981). The apparently wide range of mandibular morphologies exhibited within the known material (e.g. A.L. 288-1i and L.H.4) has been attributed by these workers to allometry and sexual dimorphism.

The naming of a new species within *Australopithecus* was justified on the basis of a variety of dental, cranial, and general skeletal features (see White, Johanson, and Kimbel, 1981). In many of these features it is claimed that the *Australopithecus afarensis* sample differs from other known australopithecines and *Homo* in having a more primitive morphology, White, Johanson, and Kimbel (1981), concluded "*Australopithecus afarensis* appears to be the most suitable known ancestor for both later *Homo* and *Australopithecus*".

*Cranial morphology of A. afarensis*

The cranial morphology of the Hadar sample is described in detail by Kimbel, Johanson and Coppens (1982) and the fragmentary Laetoli remains are described by White (1977, 1980). The facial morphology is further described by Rak (1983).

The calvaria reflects a small brain size (*circa* 500cc), large masticatory musculature and extensive pneumatisation. The occipital divides into a short broad occipital plane and a long, steeply inclined nuchal plane. The mastoids are extensively pneumatised and strongly flared, the mandibular fossae are broad and shallow and the articular eminence is small (White, Johanson and Kimbel, 1981).

The facial skeleton shows pronounced facial and subnasal prognathism, an expanded premaxillary portion curved in the sagittal and transverse planes,

nasoalveolar clivuses extending well into the nasal cavity, prominent canine/$P^3$ juga forming pillars placed lateral to the nasal aperture, the anterior roots of the zygomatic processes arise above $M^1$ or $P^4/M^1$ and the canine fossae are deep (White, Johanson and Kimbel, 1981).

Rak (1983) contrasts the morphology of the face of *A. afarensis* with that of *A. africanus* in that the former lacks true facial pillars, and the pyriform aperture has sharp lateral and inferior margins. He also notes a transverse buttress dividing the infraorbital region, a true, hollowed canine fossa, a shallow palate and a parabolic upper jaw.

*Dating of East African gracile australopithecine material*

The Laetoli australopithecine fossils were mainly surface finds. Their dating has been considered by Leakey *et al.* (1976) and is said to be in the range 3.59–3.77 m.y. B.P. whilst the Hadar hominid site is believed to be 2.9–3.3 m.y. old (Sarna–Wojcicki *et al.*, 1985).

## B. Taxonomy and Phylogeny

### Early controversies about the gracile and robust australopithecines

The discovery of the australopithecines provoked a controversy between those scientists who pointed to certain supposedly human like features as being evidence of a close relationship to man, and those who emphasised their overwhelmingly ape like morphology. The history of the australopithecine debate is described by Johanson and Edey (1981) and from a different standpoint by Ashton (1981) and Oxnard (1984). The debate has in general centred around the taxonomic implications of the gracile, rather than the robust forms.

The essential points of disagreement concerned the status and significance of the supposedly human-like features of the australopithecine cranium. These included the position and angulation of the occipital condyles (see Ashton and Zuckerman, 1952), the dental morphology and proportions (see, for example, Le Gros Clark, 1950, and Ashton, Healy and Lipton, 1957), the proportions of the articular surface of the temporal bone (see Ashton and Zuckerman, 1954, Ashton, Flinn and Moore, 1976) and the form and nature of the infraorbital foramen (see Ashton and Zuckerman, 1958). The work of Zuckerman and his colleagues served to emphasise a constellation of features which are "in some respects ape-like, and in others human. In combination, they are uniquely different from both extant groups, as distinct from lying in an intermediate position" (Ashton, 1981).

As positions polarised, the generally accepted view became that the Australopithecinae, as represented by the "gracile" South African specimens, were an ancestral form for *Homo*. The Zuckerman group, more or less alone, remained agnostic. To their minds it seemed that the morphology of these specimens represents a unique combination of features, neither ape nor man and certainly not an intermediate form (Ashton, 1981).

## Current views of the relationship of the Australopithecinae to human ancestry

The general view held by most anthropologists since the 1950's has been that one of the species of *Australopithecus* is ancestral to *Homo*. The phylogenetic scheme proposed by Johanson and White (1979) is simply that *Australopithecus afarensis* is ancestral to two later groups, *Homo* and all later australopithecines. This scheme effectively eliminates all previously known australopithecines from the direct human ancestral line and not surprisingly has received considerable criticism.

Day, Leakey, and Olson (1980) have criticised the name *Australopithecus afarensis* on formal procedural grounds. Tobias (1980b) has questioned the pooling of the Hadar and Laetoli fossils. He points out that the two sites are distant (1,600 km apart), that the fossils were found in strata of differing ages between the two sites (approx 3.6 m.y. B.P. at Laetoli and 2.6–3.1 m.y. B.P. at Hadar – date later revised to 2.9–3.3 m.y. B.P. –see above), that the size of teeth P3–M3 in the Laetoli sample is greater than that in the sample from

Hadar and that the Laetoli teeth are generally very similar to those of the South African gracile australopithecines. Tobias (1980b) concludes on the basis of a thorough comparison of dental, cranial and postcranial material that the specimens allocated to *Australopithecus afarensis* by Johanson and his co-workers are well accommodated in a taxonomic scheme which includes all of this material as geographical sub-types of *Australopithecus africanus*. He proposes that the material included within the revised range of *Australopithecus africanus* gave rise to two lineages, the robust australopithecines and *Homo*.

Zihlman (1985) has argued that the specimens included within *Australopithecus afarensis* by Johanson and his co-workers comprise not one highly sexually dimorphic species but two separate taxa. She points out that the pelvis of A.L. 288-1 shows a marked similarity to the Sterkfontein 14 pelvis "and is nearly identical in all measurements". A greater size range in limb bones exists within the *afarensis* material than within the known robust or gracile material. Zihlman demonstrates that the degree of size dimorphism is also considerably greater than that found within modern hominoids, even *Pongo*. She indicates that the hypothesis that sexual dimorphism was greater in our pre-hominid ancestor than that found within extant hominids, and that this gross dimorphic pattern was continued in *Australopithecus afarensis*, must be rejected because the dimorphism in *Pan* (which she takes to be our nearest living relative) is not so marked.

Olson (1985) has considered the morphology of occipitomastoid and nasal regions in extant and some fossil hominoids. He believes that these two regions

show independently derived specialisations in *Homo* and *"Paranthropus"* and has identified a "variety of taxonomically relevant features that unite the gracile pliocene hominids ....with *Homo*". These include the size and position of the mastoid process and associated structures, and the arrangement of sutures about the nasion. He identifies certain of the Hadar hominids as members of the *"Paranthropus"* clade (A.L. 333–45, and –105), and "Lucy", (A.L. 288–1) is designated as the lectotype of *Australopithecus africanus aethiopicus*, after Tobias (1980b). Olson's observations and interpretations of hominoid mastoid anatomy have been criticised by Kimbel, White, and Johanson (1985). They feel that inadequate attention has been paid to observable ranges of variation of the features which Olson has cited, since he accepts a wide range within *Australopithecus africanus* as acceptable whilst using a similar range in the Hadar hominids to imply a generic distinction. More recently Eckhardt (1987) has commented upon the large range of variation in the arrangement of the nasal bones which is present within hominoids suggesting that characters in this region are unsuitable for cladistic studies.

Falk and Conroy (1983) and Falk (1986) have examined the pattern and evolution of venous sinus markings in the occipital and foraminal regions of the hominoid cranium, the occipital–marginal sinus system. Falk and Conroy (1983) associate the evolution of the pattern of sinuses with the adoption of upright posture. *Australopithecus afarensis* is characterised by having enlarged occipito–marginal sinuses. In gracile australopithecines the frequency of enlarged occipito–marginal sinuses decreases and other venous routes to the vertebral

plexus are established. The robust australopithecines retain an enlarged occipito–marginal sinus. Falk takes this to imply that the robust australopithecines are descended from *Australopithecus afarensis* rather than from the gracile australopithecines. Kimbel (1984) has replied to the earlier paper from Falk and Conroy (1983) claiming lower incidences of enlarged occipito–marginal sinuses in the robust and Afar australopithecines. He has questioned the usefulness of this character in determining phylogeny "owing to marked temporal and spatial fluctuations in the frequencies of venous drainage patterns in the *Homo* lineage".

Rak (1983) in a thorough and extensive review of the form and function of the various facial morphologies presented by the australopithecines (and in later work e.g., Rak, 1985) has tended to support the views of Johanson and his co–workers. He has particularly emphasised the presence of anterior pillars, located adjacent to the pyriform aperture, in *Australopithecus africanus* and *Australopithecus robustus*. He contrasts this with *Homo* and with *Australopithecus afarensis* which are characterised by a lack of this structure. The implication is that the robust and gracile australopithecines share a derived state which tends to link them phylogenetically to the exclusion of *Homo*. The work of Grine (1985) on the morphology of the deciduous dentition has lent further support to the phylogenetic scheme in which robust australopithecines are derived from gracile ones which are in turn distinct and derived from *Australopithecus afarensis*. Grine further claims that the differences in deciduous dentition are such that the robust australopithecines are divisible into three taxa;

*Australopithecus robustus* from Kromdraai, *Australopithecus crassidens* from Swartkrans and *Australopithecus boisei* from East Africa.

McHenry (1985) has discussed the implications of post-canine megadontia for the origins of *Homo*. He lists a number of features which are shared in an apparently derived state by robust and gracile australopithecines and *Homo*. The fact that the australopithecines show a tendency to post-canine megadontia which is not manifest in early *Homo*, has been used to imply that *Homo* arose directly from *Australopithecus afarensis*. He considers that the degree of molarisation of the premolars in *Homo* lends support to the notion that increased size of the molars associated with dietary modifications that would have led to premolar molarisation might have been a characteristic of the direct ancestor of *Homo*. *Australopithecus africanus*, according to this view makes a better ancestor for *Homo* than does *Australopithecus afarensis*. This view is supported by the outcome of a cladistic study, by Skelton, McHenry, and Drawhorn (1986). Their most parsimonious cladogram is compatible with a phylogenetic scheme in which robust australopithecines and *Homo* arise from *Australopithecus africanus* which in turn arises from *Australopithecus afarensis*. However the second most parsimonious cladogram from this study is only marginally less so than the first (44 of 69 traits, as opposed to 45 of 69 traits). It lends support to the phylogenetic scheme of Johanson and his co-workers which has *Homo* arising direct from *Australopithecus afarensis*. A recent reconsideration and reanalysis of the same data by Wood and Chamberlain (1987) has indicated that when homoplasy is taken into account Skelton *et al.*'s

second most parsimonious cladogram is in fact more parsimonious than their first.

A thorough cladistic analysis of a variety of fossil hominids by Wood and Chamberlain (1986) failed to resolve the issue of the relationship of *Australopithecus africanus* to *Homo*. These workers concluded that the australopithecines may form a clade, alternatively *Australopithecus africanus* may be the sister group of *Homo*, leaving *A. afarensis* as the sister group of the "robust" australopithecines. Their study demonstrated that homoplasies are common and that these confound cladistic techniques which treat all characters equally,

A more recent study by these workers (Chamberlain and Wood, 1987) shows a more consistent joining of *Australopithecus africanus* with robust australopithecines to form a clade.

The most recent of the series of cladistic studies by Wood and Chamberlain (1987) has concentrated on the relationships of the robust australopithecines to *A. afarensis*, *A. africanus*, and *Homo*. The outcome of cladistic analysis using an improved program supports the "grade" cladogram first proposed in their 1986 paper. They suggest that "*A. afarensis* may be too derived to represent the common ancestor of all known hominids".

As noted above, Grine (1985) claims that the differences in deciduous dentition morphology in the robust australopithecines are such that they are divisible into three taxa; *Australopithecus* ("*Paranthropus*") *robustus* from

Kromdraai, *Australopithecus crassidens* from Swartkrans and *Australopithecus boisei* from East Africa. This position has been strengthened by the observation of different allometric patterns in the adult cusp morphologies in these same groups (Jungers and Grine, 1986). Grine's (1985) work on the deciduous dental morphology of "robust" australopithecines led him to conclude that the "evidence suggests *A. robustus* to have been ancestral to *A. crassidens*" and that *A. boisei* evolved from an *A. crassidens*–like ancestor.

Some recent studies seem to link together morphological patterns within *Homo* and the robust australopithecines. Dean and Wood (1981, 1982) have undertaken a detailed study of the anatomy of the basicranium in extant and fossil hominoids. An observation of this work has been that there is an apparent parallelism in the basicranial morphologies of *Homo sapiens* and robust australopithecines. Both share a relatively forward placed foramen magnum and a more coronally orientated petrous bone. This contrasts with the *Australopithecus africanus* morphology which is ape–like.

Dean (1985, 1986) has added to the list of similarities the eruption pattern of the permanent teeth. He has claimed that in "*Paranthropus*" and *Homo* the incisors and first molar seem to erupt nearly simultaneously whilst in apes, *A. afarensis* and *A. africanus* the first molar appears before the incisors. He considers (1986) the phylogenetic implications of this possible synapomorphy and indicates that it would suggest that "*Homo* and '*Paranthropus*' share a common ancestor to the exclusion of *Australopithecus*". He states that this suggests that the australopithecines might be two separate genera. Grine (1987) has, however,

disputed the observational basis of Dean's claim for equivalent eruption times for the incisors and first molar in *"Paranthropus"*. He states that the observations made on one of Dean's four specimens were clearly erroneous and that the situation is ambiguous in the others. Dean's (1985, 1986) case is further weakened by the work of Holly Smith (1986) who made an extensive comparison of patterns of dental development in hominoids and concluded that "*A. robustus* and *A. boisei* share a unique pattern (of dental development) that is neither human nor pongid".

A more recent development concerning the relationships of the australopithecines has been the discovery of a putative 2.5 million year old *Australopithecus boisei* cranium from the west of Lake Turkana in Kenya (Walker, Leakey, Harris, and Brown, 1986). The dating of this specimen, which has not yet been seriously challenged, makes this the oldest example of a robust australopithecine. It is argued that its age makes it unlikely that *A. boisei* is derived from *A. robustus* and that robust australopithecines are derived from *A. africanus*, (contra Rak, 1983, and Johanson and co-workers, see above). Delson (1986) has commented on this discovery. He feels that the allocation of this cranium to *A. boisei* is not fully supported and that further assessment is warranted. The influence of this discovery on phylogenetic schemes of the hominids is yet to be seen (see Walker, 1987, Leakey and Walker, 1988).

# EARLY HOMO AND HOMO HABILIS

## A. Morphology and Provenance

The discovery of *Australopithecus boisei* in Olduvai Gorge in the late 1950's prompted intense paleontological activity in the region. Finds were also made of remains of a creature which appears to be distinct from the robust australopithecines (Leakey, 1960, 1961a, 1961b) and which later formed the basis for the naming of a new species within *Homo*, *Homo habilis* (Leakey *et al.*, 1964). The holotype of the new species comprised the OH 7 mandible, parietals and hand bones and the description was based upon these plus the paratype specimens, OH 4 (mandibular fragment), OH 8 (foot and hand bones), OH 6 (cranial fragments) and OH 13 (fragmentary skull).

Since this first description of the new species a variety of fossils from East and South Africa have been attributed to early *Homo* and either assigned to or associated with *Homo habilis* (see Chamberlain, 1987). These include specimens from Olduvai (see Oakley *et al.*, 1977), Koobi Fora (see Oakley, *et al.*, 1977, Walker and Leakey, 1978), Swartkrans (Clarke *et al.*, 1970, Clarke, 1977), Sterkfontein (Hughes and Tobias, 1977) and Omo (Boaz and Howell, 1977). Most notable amongst these are the specimens KNM-ER 1470, OH 24, OH 62, STW 53, and a composite cranium SK.80/846/847. There is little value in considering each of these fossils separately in the context of this thesis. I shall instead concentrate on a brief description of the material which is studied in this current work.

Olduvai Gorge has, since the first announcement of *Homo habilis*, yielded a variety of remains which have been attributed to this taxon (see Oakley *et al.*, 1977, and Day, 1986, for a recent list). The remains include a cranium, O.H. 24 (Leakey, Clarke and Leakey, 1971) found in the lower part of Bed I. The skull was severely crushed and distorted and somewhat incomplete. It has been reconstructed by Clarke (see previous reference) and although this has been largely successful some distortion of the vault and face remains (Tobias, 1980a).

Further discoveries which have been associated with early *Homo* have been made at East Turkana, Kenya (Day and Leakey, 1973, Leakey and Wood, 1973, Day and Leakey, 1974, Leakey and Wood, 1974, Day *et al.*, 1975, Day *et al.*, 1976, Walker and Leakey, 1978). Significant amongst these are two fragmented but reconstructed crania, KNM–ER 1470 and KNM–ER 1813. KNM–ER 1470 has a cranial capacity of about 750 cc. and KNM–ER 1813 of about 510 cc. (Holloway, 1983). The precise taxonomic attribution of these crania is a matter of current debate and is considered further below.

It was noted earlier that some fossil remains from South Africa have been associated with early *Homo* (cranial remains from Sterkfontein and Swartkrans). The Swartkrans site has yielded material that was initially attributed to *Australopithecus robustus* and *Telanthropus* capensis (Broom and Robinson, 1949). More recently it has been noticed that some of this material (SK 80, SK 846, and SK 847) fits together to make a composite cranium (Clarke, Howell and Brain, 1970). This composite cranium (collectively known as SK 847) has been

compared to and considered to be possibly conspecific with OH 13 (a putative *Homo habilis*) by Clarke and Howell (1972).

Sterkfontein has yielded a partial cranium, StW 53 which is said to bear strong affinities to *Homo habilis* (Hughes and Tobias, 1977). Its cranial capacity appears to be larger than that of *Australopithecus africanus* and smaller than *Homo erectus* (Tobias, 1978b).

The most recent fossil find to have been likened to *Homo habilis* comprises parts of a skull, right arm, and both legs recovered from lower Bed I, Olduvai Gorge, Tanzania (Johanson *et al.*, 1987). The postcranial skeleton has been compared with that of *Australopithecus afarensis* and the face palate and dentition have been reported as showing "strong morphological similarities ... to *Homo habilis* (especially StW 53)" (Johanson *et al.*, 1987). Wood (1987) has commented that "the logical "trail" becomes tenuous because StW 53 has merely been likened to *Homo habilis*, and not formally attributed to it".

## Cranial morphology of *Homo habilis*

Recent studies (reviewed below) have led to the suggestion that two or more taxa are represented by the material which has been allocated to early *Homo* and *Homo habilis*. It is therefore impossible to give a description of the typical cranial morphology of this group of fossils.

The only cranial remains included in the original description of *Homo habilis* were the OH 7 cranial fragments (parietals) and mandible (type), the OH 13 adolescent partial cranium, the OH 4 mandibular fragment and the OH 6

cranial fragments (paratypes) (Leakey *et al.*, 1964). In the same publication the OH 14 fragments of a juvenile cranium and the fragmentary skull OH 16 were referred to the new species. OH 16 has been subsequently formally withdrawn from *Homo habilis* (Tobias, 1965) and the status of OH 14 is in doubt.

The cranial morphology of the original hypodigm of *Homo habilis* was said to differ from *Australopithecus* in having smaller mandibles and maxillae, a larger cranial capacity (about 600 cc), no marked post-orbital constriction, a less marked external sagittal curvature of the occipital, and in a number of dental features (smaller molars, bucco-lingually narrowed premolars, canine large relative to premolars) (Leakey *et al.*, 1964).

Later material which has been considered to represent early *Homo* and which is included in the study of cranial morphology described later in this chapter includes OH 24 and KNM-ER 1470.

OH 24 has been distinguished from the australopithecines on the basis of less postorbital constriction, a higher frontal, wider parietal bones and more *Homo*-like mandibular fossae and nasal bone structure (Leakey, Clarke, and Leakey, 1971). Its estimated cranial capacity is in the region of 590 cc (Holloway, 1983). This specimen is heavily reconstructed and has suffered some distortion (Tobias, 1980a).

KNM-ER 1470 has been reconstructed from a considerable number of isolated fragments. It appears to have had a cranial capacity in the region of 750 cc. (Holloway, 1983) which is considerably larger than most specimens allocated

to *Homo habilis*. The vault of KNM–ER 1470 is reasonably complete, it is domed with steeply sloping sides and parietal eminences, the glenoid fossae and external auditory meatus are positioned well forward relative to *Australopithecus* and there is no indication of strong nuchal or sagittal crests. There is only moderate postorbital waisting and no evidence of marked temporal lines. The apex rises considerably above the weakly developed supra orbital tori.

The face is less complete and its orientation is uncertain. The alveoli are large and suggest large teeth. The palate is shallow, broad and short. The basicranium is incomplete and damaged (Leakey, 1973).

## Dating

The dating of the South African hominid bearing localities has been considered earlier. In the context of this thesis the most important localities are Olduvai and Koobi Fora.

The majority of material which is attributable to *Homo habilis* (including OH 7 and OH 24) has been recovered from Olduvai Gorge Bed I. Other material (including OH 13) comes from bed II. The Bed I material was located between tuffs dated in the range 1.8–1.9 m.y. B.P. and the Bed II material between tuffs dated 1.55–1.7 m.y. B.P. (Leakey and Hay, 1982)

KNM–ER 1470 and ER 1813 were found below the KBS tuff which originally was believed to date from 2.6 million years B.P. (Fitch and Miller, 1970). More recent attempts at dating have suggested a younger date of about 1.8–1.9 million years B.P. (McDougall, 1985, McDougal *et al.*, 1985).

## B. Taxonomy and Phylogeny of Homo habilis

The name *Homo habilis* was first proposed by Leakey, Tobias and Napier (1964) and was applied to a variety of fossil remains recovered from Bed I and lower Bed II Olduvai Gorge. These workers, in constructing this new taxon revised the current definition of the genus *Homo* to include a reduced cranial capacity (600 cm3) and a variety of postcranial and cranial features. This they justified in order to include the new material in *Homo* rather than name a distinct genus for it. The designated type specimen was a mandible, vault and hand bones, OH 7. It was claimed to differ from *Australopithecus* in having larger incisors, narrower premolars, smaller molars and a "marked tendency towards bucco-lingual narrowing and mesiodistal elongation of all the teeth". *Homo habilis*, it was further claimed, had a mean cranial capacity greater than that of *Australopithecus* but smaller than that of later *Homo*, a variable degree of cranial muscular markings, a less curved occipital bone than the australopithecines and *Homo erectus*, and a parietal bone with a sagittal curvature intermediate between hominines and australopithecines.

Robinson (1965) was amongst the first to question the validity of this new species. He examined the adequacy of the original "differential diagnosis" and criticised the revised definition of *Homo* since it "depends in part on the validity of the new species proposed for it". He further took issue with evidence for the making of a dental distinction between the new taxon and the australopithecines and *Homo erectus*, presenting data that fail to demonstrate a great difference between the O.H. 7 dental shape and that of the australopithecines. Robinson

felt that there was an "insufficient morphological distance" between *Homo erectus* and *Australopithecus* to justify the insertion of a new species. There ensued a debate in which the taxon was vigorously attacked and defended, (Leakey, 1964, Le Gros Clark, 1964, Oakley, 1964, Oakley and Campbell, 1964, Tobias, 1964, Pilbeam and Simons, 1965, Robinson, 1965, 1966, Howell, 1967).

There have been several attempts in recent years to assess the homogeneity of those fossils assigned to or compared with *Homo habilis*. An interesting study of the basicranial anatomy of Plio–Pleistocene African hominids has been undertaken by Dean and Wood (1981 and 1982). The study included a metrical analysis of the basicranium in a variety of hominids. The cranial base of, amongst others, OH 24 was found to show a "combination of features some of which are characteristic of the "robust" australopithecines, and others of which are seen in *Homo erectus* and in the modern *Homo sapiens* sample". The petrous angle and sphenoid length/width ratio was more indicative of the pattern seen in *Homo erectus*. The cranial base pattern of KNM–ER 1470 (which is largely missing) and of KNM–ER 1813 resemble *Homo erectus*, but KNM–ER 1813 is smaller and has a relatively shorter sphenoid than KNM–ER 1470.

More recently Stringer (1985) has reviewed the evidence for *Homo habilis* and has made some further studies of his own. He has examined the range of variation of endocranial volumes for a variety of specimens attributed to early *Homo* and has demonstrated that the coefficient of variation would equal 12.4 if KNM–ER 1813, OH 24, OH 13, OH 7, KNM–ER 1470 and others were to be included within a single taxon. This compares with a C.V. of between 8.9

and 10.9 for modern hominoids. He compiled the dental dimensions of a variety of hominids and summarised an earlier study by Wood and Abbott (1983) and Wood, Abbott and Graham (1983) in which the morphology of a variety of hominid molars was examined. He concluded that the early *Homo* sample was generally distinguished by relatively narrow teeth but that the upper dentition seem most derived in this feature. He felt that his compilation of dental data provided little basis for dividing up the early *Homo* sample.

Stringer went on to examine a variety of midsagittal and transverse facial angles in modern *Homo* and *Pan* and in several early *Homo* crania (including OH 24, KNM-ER 1470, and KNM-ER 1813). He concluded that KNM-ER 1470 and KNM-ER 1813 both show angles which appear derived in the direction of *Homo* though some angles in KNM-ER 1470 seem more derived in the direction of the australopithecine clade. The differences in the angles between these two crania are not of the same type as those found in sexually dimorphic modern hominoids. The cranial angles of OH 24 are in general more like those of Sts 5. The overall results of this study suggested to Stringer "at least three Plio-Pleistocene species of early *Homo*".

Wood (1985) has reviewed the systematic relationships of early *Homo* in Kenya. He has examined a variety of features of the cranial vault, base, and face in KNM-ER 1470, KNM-ER 1813, and *Australopithecus africanus*. He details a number of features in which both of the Kenyan fossils differ from the gracile australopithecines and compares the two putative early *Homo* crania with each other. He found that they differ in facial morphology more than

KNM–ER 1813 differs from *Australopithecus africanus* as assessed by Mahalanobis' $D^2$. He suggests that the observed difference in cranial capacity would place these two crania at the limit of acceptable variation as judged by that found in modern and some fossil hominoids and suggests that "differences in size and shape between the two crania may merit their assignment to two taxa".

Recent work by Chamberlain (1987) and Chamberlain and Wood (1987) has further served to emphasise the dishomogeneity of the material currently considered to represent early *Homo*. A number of cranial and dental dimensions were used to determine phenetic groupings of material attributed to either *Homo habilis* or *Homo sp. indet.*. The outcome of this study suggested that OH 7, OH 13, and OH 24 could reasonably be accommodated in *Homo habilis* whilst KNM–ER 1470 and KNM–ER 1813 appeared distinct. Cladistic analysis of a number of hominid groups including the redefined groupings of early *Homo* resulted in a cladogram in which "*Homo sp.* (includes KNM–ER 1470 and 1813) is most parsimoniously interpreted as the sister taxon of the "robust" australopithecines, with *A. africanus* as the sister taxon of this clade. *H. habilis*, on the other hand, appears to be a relatively primitive hominid that nonetheless shares some derived characters with other post–*A. afarensis* hominid taxa".

Further evidence in support of variability within early *Homo* comes from a phenetic study of the facial region of fossil hominids by Bilsborough and Wood (1988). They conclude that KNM–ER 1813 shows similarities with OH 24 in facial dimensions, though not necessarily in other cranial regions whilst

KNM-ER 1470 "displays a remarkable facial morphology some aspects of which are reminiscent of 'robust'australopithecines".

From these studies it seems possible that *Homo habilis* has had assigned to it a range of material which is too variable to be comfortably accommodated within a single species. It may well be that a number of species are represented. The resolution of questions relating to the number of taxa and their phylogenetic relationships awaits further material and further study.

## *HOMO ERECTUS*

### A. Morphology and Provenance

A wide range of fossil material from Asia, Africa and Europe has been attributed to *Homo erectus*. The fossil remains have, in common, a variety of features, some of which may well be purely plesiomorphous (see later).

#### *Homo erectus* in Asia

##### *Java*

The first discovery of material now attributed to this taxon was made in 1891 at Trinil, by the Solo river, Java (Dubois, 1891). The material from Trinil includes a thick boned calotte and some femoral remains with disputed associations (Day and Molleson, 1973, Jourdan, 1984). Dubois (1894) named a new species and genus, *Pithecanthropus erectus*, on the basis of this material. Weidenreich (1940) has since accommodated it within *Homo erectus* but has given it subspecific status *Homo erectus javensis* whilst Dobzhansky (1944) included it within *Homo erectus erectus*.

Further Javanese material which may be conspecific includes a juvenile cranium from Modjokerto (von Koenigswald, 1936, Tobias and von Koenigswald, 1964 but see Jacob, 1982–*Pithecanthropus modjokertensis*) and certain of the finds from Sangiran, (e.g. Sangiran 2, Oakley *et al.*, 1975). Day (1986) lists some thirty specimens which have been recovered from Sangiran including, partial crania, mandibles, and teeth. The *Pithecanthropus* IV (Sangiran 4) calvarium, maxilla and teeth have been attributed to a different group (*Pithecanthropus*

*robustus*) from the Trinil remains by von Koenigswald (1950). Campbell (1964) has, however, lumped Sangiran 4 and the Trinil remains together.

Two Javan sites, Ngandong and Sambungmachan, have yielded fossil evidence of a hominid whose morphology is in some respects like that of *Homo erectus* and in others (e.g. cranial capacity) more like *Homo sapiens*. This material has at various times and by various workers been attributed to *Pithecanthropus soloensis* (Jacob, 1982), *Homo sapiens soloensis* (Orchiston and Seiser, 1982) and *Homo erectus* (Santa Luca, 1980, Pope and Cronin, 1984)

*Dating of Javanese sites*

The determination of dates for these Javanese fossils has proved a considerable problem.

The Trinil and Sangiran remains have been recovered from two beds, the older is termed the Pucangan, the younger the Kabuh. The Trinil material and the Sangiran material of more recent aspect have been recovered from the Kabuh beds which have been dated at about 0.5–0.83 m.y. B.P. (von Koenigswald, 1964). The older Sangiran (e.g. Sangiran 4) material was recovered from the Pucangan bed which has been dated at 0.8–1.3 million years (Pope and Cronin, 1984). The dating of the Ngandong and Sambungmachan material is highly problematical (Semah, 1982) though Bartstra (1983) has suggested that it may be relatively young (from the Upper Pleistocene).

*China*

Further material attributed to *Homo erectus* has been discovered in China. The major finds were made at Zhoukoudian (Choukoutien) (Weidenreich, 1936, 1937a,b, 1941b, 1943, Black, 1931) and included calvaria, teeth, mandibles and postcrania from about 50 individuals. Most of this pre-war material was later lost during the upheavals of the 1940's. Renewed excavations have, however, resulted in the discovery of several teeth, cranial, mandibular, and postcranial fragments (Woo and Chao, 1954, Woo and Chao, 1959, Chiu *et al.*, 1973).

Further finds from China include a calvarium, cranial and mandibular fragments and several teeth from Hexian (Huang *et al.*, 1981, Wu, 1983), teeth from Yuanmou, Yunxian County, Yunxi County and Nanzhao County (Wu, 1981), a mandible, a tooth, and a partial cranium from Lantian (Woo, 1964, 1965)

A cranium has been recovered from Dali, Shaanxi province (Wang *et al.*, 1979). It was initially allocated to *Homo erectus* though more recent studies have suggested it has a number of more sapient features and that it could be related to other non-*erectus* Chinese material (Wu, 1981).

*Dating of Chinese sites*

The dating of the Zhoukoudian cave deposits is problematical. Faunal correlation indicates an age of about 400,000 years B.P. (Kurten, 1959) whilst Wu (1981), in summarising data from fission track, uranium thorium series, paleomagnetism, and thermoluminescence, dates the upper layer at 230,000 years B.P. and the lowest at 0.5 m.y. B.P. Faunal correlations between the Hexian

site and Zhoukoudian layers indicate a date of about 0.25 m.y. B.P. (Xu and You, 1984)

The Lantian material has been attributed to an earlier period than that from Zhoukoudian (in the region of 0.5–0.8 million years B.P., Liu and Ding, 1984) and the Dali cranium has been given a later date (0.128–0.25 m.y. B.P., Liu and Ding, 1984)

*Homo erectus* from Europe

A number of fossils from Europe have been compared with the *Homo erectus* material from China.

The putative *erectus* material includes, amongst other, more scattered and fragmentary remains (see Howells, 1980), a mandible from Heidelberg (West Germany), cranial fragments from Bilzingsleben (G.D.R), a cranium from Petralona (Greece) some deciduous teeth and an occipital fragment from Vertesszollos, (Hungary) and some cranial, mandibular, and pelvic fragments from Arago, (France).

In general, however, the material is not identical to the Asian specimens and some may show a number of derived "Neanderthal" or *Homo sapiens* characters (Stringer, 1984). Howell (1976), Andrews (1984) and Stringer (1984) have concluded that *Homo erectus* cannot be recognised in Europe at all. The affinities of this material will be considered in more detail below.

## *Homo erectus* from Africa

Various workers have described *Homo erectus*–like remains from South, East and North Africa.

### *Southern Africa*

The southern African evidence for this taxon rests with two groupings of material.

1. Those remains which have been recovered from Swartkrans and which were originally assigned to *"Telanthropus"* (e.g. SK 15). More recently it has been suggested that at least some of this material is more closely related to *Homo habilis* (see previous section).

2. The Kabwe cranium and associated finds, the Cave of Hearths mandible and the Hopefield calvaria (Oakley *et al.*, 1977) from southern Africa, together with the Bodo skull from Ethiopia. These may represent a single population (Howells, 1980) which has been (contentiously) ranked as *Homo erectus* (Coon, 1962 but see Brose and Wolpoff, 1971).

### *East Africa*

Several fossilised remains which have been likened to *Homo erectus* have been recovered from Olduvai Gorge. The most complete cranial fragment is a calvarium, O.H. 9. recovered from Upper Bed II (Leakey, 1961a). Other material from Olduvai which has been attributed to *Homo erectus* includes cranial and mandibular fragments, dental remains, a femoral shaft and a partial hip bone

(see Day, 1986 for a full list) from various sites and from Beds II and IV.

East of Lake Turkana, Kenya, from the Koobi Fora region a number of significant finds of cranial and postcranial material attributed to *Homo erectus* have been made. These include a well preserved cranium, KNM–ER 3733 (Leakey, 1976), a calvarium, KNM–ER 3883 (Walker and Leakey, 1978) and a number of teeth, mandibles, and postcranial bones (Howell, 1978).

More recent work on the west side of Lake Turkana has uncovered a remarkably complete skeleton of a youth, KNM–WT 15000, which has been attributed to the same taxon as the East Turkana material described above (Brown, Harris, Leakey, and Walker, 1985).

Other East African material which has been attributed to or associated with *Homo erectus* includes the Ndutu cranium from Tanzania (Clark, 1976, but see Brauer, 1984), the Kapthurin mandible from Baringo (Leakey *et al.*, 1969 but see Howells 1980) and cranial fragments from Member K of the Shungura formation, lower Omo Basin and Gombore II on the Awash river both in Ethiopia (Howell, 1978).

*Northwest Africa*

Material from North Africa which has been attributed to *Homo erectus* includes mostly mandibles, but also teeth and cranial bones from Ternifine, Algeria, Thomas Quarries, Sidi Abderrahman, and Rabat, Morrocco and a calvaria from Sale, Morocco, (Howells, 1980). The attribution of this material to *Homo erectus* is a matter of debate (see Howell, 1978, Howells, 1980).

*Dating of African sites*

Considerable doubt exists regarding the presence of *Homo erectus* in Africa (see below). The best preserved remains have come from Olduvai and Koobi Fora.

The OH 9 calvaria was located above tuffs dated 1.25 m.y. B.P. and below the lower part of Bed III (1.2 m.y. B.P., Leakey and Hay, 1982). The Bed IV material was found between strata dated 0.75 m.y. B.P. and 0.6 m.y. B.P. (Leakey and Hay, 1982).

The Koobi Fora material was found between tuffs dated between 1.3 and 1.85 m.y. B.P. (Brown *et al.* 1985) and the KNM–WT 15000 skeleton is dated at about 1.6 million years B.P. (Brown, Harris, Leakey, and Walker, 1985).

The cranial morphology of specimens attributed to *Homo erectus*

It is clear from the foregoing discussion that the name *Homo erectus* has been applied to a very wide range of material from different localities and with different morphologies. It is therefore impossible to give an all–encompassing description of the cranial morphology of this taxon. I shall, instead, concentrate on a general description of those cranial features which seem to unite the material described above (this will inevitably include symplesiomorphous as well as synapomorphous characters) and follow this with a discussion of the differences encountered between those fossils included in the study presented later in this chapter.

*General Morphology* (Howell, 1978 unless otherwise indicated)

The bones of the vault are thick especially in the bregmatic region. This is associated with marked parasagittal depressions. The maximum vault breadth is at or toward the cranial base. The frontal is low and receding and the parietal is flatter longitudinally and more angular transversely than in *H. sapiens* and may show a true angular torus (Stringer, 1984), the occipital is sharply angulated with the upper scale generally shorter than the lower and with a marked torus. The general cranial shape is long and low (Stringer, 1984).

The foramen magnum is angulated between its nuchal and basisphenoidal planes, the foramen lacerum and the petro–occipital fissure may be absent, the carotid canal is small. The mandibular fossa is deep, short and set relatively laterally, the auditory meatus is on or just above the nasion–opisthion line, the mastoid is variable in size and may be large with a projecting anterior portion and the posterior portion may form a lateral bulge of the cranial wall.

The facial skeleton has a heavy, projecting supraorbital torus continuous with the glabellar torus. There is a distinct supraorbital tubercle and these may be a supratoral sulcus. The infraorbital margin is rounded and at the same level as the orbital floor. The face is relatively small though broad and is moderately to slightly prognathous with reference to australopithecines. The nasal bones are wide and the maxilla has a strong anterior facies and alveolar processes.

*Javanese material – SANGIRAN 4*

The Sangiran 4 cranium is represented by a vault comprising the posterior 3/4 of the parietals, an entire occipital including the foramen magnum, and the maxillae. It differs from the condition described above in displaying, in the reconstruction, a very low vault, a marked frontal keel, a large occipital torus continuous with the supramastoid ridges and in having extremely well developed muscular ridges. There is considerable alveolar prognathism and the zygomatic bones arise near the alveolar borders. Its cranial capacity is estimated at 908 cc. (Holloway, 1981).

*Chinese material – "Sinanthropus pekinensis"* (Black, 1927)

The Chinese material differs from the Javanese in several ways. The average cranial capacity is greater (915cc. to 1225cc., Weidenreich, 1943), the skulls have a more rounded supraorbital torus and a higher forehead, the teeth are smaller, the palate is more rounded, and the occiput is less angular.

*African material – KNM–ER 3733*

Stringer (1984), Wood (1984) and Rightmire (1984a) have noted that KNM–ER 3733 differs from the Asian representatives of this grade in having different proportions of the occipital bone, no fissure separating the mastoid from the petrosal crest of the tympanic, less well defined metopic, coronal, sagittal and bregmatic prominences, no true angular torus on the parietal, a less robust tympanic plate, thinner vault bones, a smaller interorbital breadth and a longer

narrower face. Holloway (1983) has estimated this cranium to have a capacity of 848 cc.

## B. Taxonomy and Phylogeny

The term *Homo erectus* was first applied to certain of the remains from Java and China (Weidenreich, 1940). Since this time, however, it has been applied to a number of remains from a wider geographical range (see above and Howells, 1980).

The extension of usage of the nomen to include material from Europe and Africa has been a source of debate. Stringer (1984) has considered the cladistic relationships between the putative "*erectus*" material of Europe, *Homo erectus* from Asia, supposed African members of *Homo erectus*, and Neanderthals and modern humans. He concludes that only a grade definition of *Homo erectus* built around a variety of general features, many of which are plesiomorphous, can practicably include the African and Asian material. Only the Chinese and Javanese fossils (excluding Ngandong) are satisfactorily defined by a suite of derived characters. The early African fossils "would have to be regarded as primitive members of this grade lacking many of the specialised characters linked with increased robusticity in the later Asian forms". Of the European material which he examined, including the Petralona, Arago, Bilzingsleben and Vertesszollos specimens, he claims that "departures from the *Homo erectus s.s.* condition predominate over resemblances in diagnostic characters". He states that, overall the evidence favours the classification of hominids such as Petralona

and Arago as *Homo sapiens s.l.*

Wood (1984) has further examined the cladistic relationships of material from Africa and Asia which has been included in *Homo erectus*. He defined the taxon on the basis of the Asian remains and identified a number of autapomorphies including features of the occipital torus, the frontal bone, and the ratio between occipital and parietal arcs. He states "preliminary assessment suggests that the morphology of the occipital and frontal regions of KNM-ER 3733 and 3883 is not sufficiently characteristic (with the exception of the occipital-parietal arc ratio) of *H. erectus* (sensu stricto) to merit their automatic inclusion in *H. erectus*".

The results of Stringer's and Wood's studies are strongly suggestive of the need to make a distinction between the cladistic view of *Homo erectus* which is able to define only certain of the Asian material by autapomorphies and the gradistic view which defines a more widespread distribution by a number of plesiomorphous characters.

The contrasting view is given by Rightmire (1984a) who compared the East African "*erectus*" material with that from Trinil and Sangiran. He indicates that the anatomy of the tympanic plate and glenoid cavity is broadly similar in all these specimens and that this differs from that found in *Homo sapiens*. He finds similarities in the flexion of the occipital and in the presence of a transverse torus and states "while there is variation in all these features, consistent regional distinctions are not easily defined". He indicates that the Asian sample exhibits more sagittal keeling, some differences in the shape of the

supramastoid crest and a more robust tympanic plate than the East African but concludes that the "evidence suggesting overall similarity in form is much more striking".

A synthetic view is given by Bilsborough and Wood (1986). They performed a phenetic and a cladistic analysis of "early" *Homo erectus* from East Africa, "late" *Homo erectus* from Zhoukoudien and Indonesia, a number of australopithecines and habilines, certain European Neanderthals, and a collection of modern human crania. The phenetic studies "suggest a distinct break between "early" East African H. *erectus* and the earlier non-*erectus* remains". These studies also demonstrated morphological differences between the "early" African and "late" Asian *Homo erectus* groups. These were, however, less than those between the "early" African *Homo erectus* specimens and KNM-ER 1470 or *Homo habilis s.s.*. Cladistic analysis suggests that *Homo erectus s.s.* has to be defined by fewer characters than is normally the case and if the definition is restricted to autapomorphies one of the authors (Wood) feels that only OH 9 is a suitable East African candidate for inclusion in this taxon. Bilsborough and Wood differ in their evaluation of the relative utility of cladistic and phenetic methods but agree that there is good evidence of temporal variation within *Homo erectus*. Bilsborough sees continuity between *Homo erectus* and *Homo sapiens*, Wood interprets the evidence as suggesting that *Homo habilis* "has equal, if not greater, claims to be regarded as the sister group of *Homo sapiens*".

## *HOMO SAPIENS*

### A. Morphology and Provenance

Worldwide there has been a considerable amount of material recovered which spans the period between the existence of *Homo erectus* and the current geographic subgroups of *Homo sapiens sapiens*. Evidence from mitochondrial DNA suggests that the races of mankind share a common African female ancestor some 200,000 years ago (Cann *et al.*, 1987, also see Stringer, 1984, p. 123 and Stringer and Andrews, 1988). Unfortunately genetic evidence says nothing direct about the morphology of our common ancestor, for this we have to examine the fossil record.

In the preceding section it was noted that fossils attributed to *Homo erectus* span the time range 1.7–0.2 m.y. B.P. This time range overlaps that from which there is evidence of "early archaic" *Homo sapiens* (see Day and Stringer, 1982, Stringer, 1987b, Brauer, 1984). Examples of crania which are attributed to this group by some (e.g. the Petralona cranium, Stringer, 1987b) have already been discussed in the preceding section. In this section I shall attempt a summary of those groups of fossils which existed either contemporaneously with representatives of (at least Asian) *Homo erectus* or in the intervening span between *Homo erectus* and the current geographical subgroups of *Homo sapiens sapiens*. I shall first list the material by geographical region, grouping fossils by what has been said of their morphology and dating. Later I shall attempt to bring this material together in a synthetic review of what has been said of its phylogeny. This consideration is by necessity brief, its purpose being to set the

scene for the later parts of this chapter. More space is devoted to the material which is studied later than to the groups which are not sampled.

## The geographical distribution of fossil *Homo sapiens*

### Africa

#### *Early archaic Homo sapiens*

Earlier in this chapter I have mentioned the material from Ternifine, (Algeria) and from Thomas Quarries, Sidi Abderrahman, Rabat and Sale (Morocco) which has been considered to represent *Homo erectus* (but see Howells, 1980 and Howell, 1978). Brauer (1984) places most of these fossils in the span 0.45–0.2 m.y. B.P. whilst Hublin (1985) places the Ternifine material at about 0.6 m.y. B.P. Further African material which spans roughly the same time includes that from Bodo, Ndutu, Hopefield (Elandsfontein) and Kabwe 1 (Broken Hill 1) (0.4–0.125 m.y. B.P., Brauer, 1984). This latter grouping of material (? + Rabat, see Brauer, 1984, Rightmire, 1980) has been considered to represent "early archaic *Homo sapiens*" together with specimens such as Petralona and Arago from Europe (Brauer, 1984, Rightmire, 1984b, Stringer, 1987b) though other workers may disagree (e.g. Ndutu, Clarke, 1976). The Kabwe 1 (Broken Hill 1) cranium from Zambia is included in this study.

*Cranial Morphology of Kabwe 1* (based upon Howell, 1978)

The cranium has a low vault and is long and ovoid. The vault bones are thinner than those of *Homo erectus* (see earlier). The frontal is low and relatively flattened (Brauer, 1984) and there is a metopic ridge. The superior temporal lines are strongly marked. The occipital is sharply angled with the lower scale flat and the upper transversely curved. The occipital torus is strong, narrowing laterally. There is no evidence of an occipital bun (Rightmire, 1980). The foramen magnum is long relative to its breadth and the occipital condyles are long and narrow. There is a small foramen lacerum and narrow foramen ovale. The mandibular fossa is wide and deeply concave and the articular eminence is broad and low.

The face, placed below a massive, laterally projecting supraorbital torus with a swollen, downwardly displaced glabellar portion, is long, particularly in the maxillary alveolar portion. The orbits are large, deep and approximately quadrangular, the interorbital region is wide and the naso–frontal process of the maxilla is strongly developed. The nasal aperture is broad and rounded. The palate is U–shaped, deep and displays high, robust alveolar processes. The maxilla shows only a faint suborbital (canine) depression (Brauer, 1984). The malar region is massive and low set, with a broad root of the zygomatic arch. Cranial capacity is estimated at over 1250 cc. (Howell, 1978).

Klein (1973) has, on the basis of an evaluation of associated artifacts and fauna suggested a minimum age of 125,000 years for the Kabwe cranium.

*Late archaic Homo sapiens*

From various sites in Africa there have been recovered a number of cranial remains which have been attributed to a group of "late archaic *Homo sapiens*". These include the cranial and dental remains from Djebel Irhoud (Jebel Ighoud), Morocco, the Laetoli Hominid 18 cranium from Tanzania, certain of the cranial remains from the Omo river region, Ethiopia (Omo I, ?Omo II, Rightmire, 1984b, Brauer and Leakey, 1986, though Day and Stringer, 1982, regard Omo I as being anatomically modern), the ES–11693 cranium from Kenya (Brauer and Leakey, 1986) and the Florisbad cranium, from South Africa (for a more complete catalogue see Brauer, 1984, Stringer, 1987b and in press, Rightmire, 1984b).

These crania display a more "modern" morphology than representatives of "early archaic *Homo sapiens*". In general they have a larger cranial capacity, a more rounded and expanded vault, less cranial robustness including smaller supraorbital and occipital tori and less occipital angulation, a more curved frontal and a lighter facial morphology including less heavily built maxillae. They are dated in the range 150–40 t.y. B.P. (see Brauer, 1984, Rightmire, 1984 for dates and morphology). No representatives of this sample are included in this study.

*Anatomically modern Homo sapiens*

As from most regions of the world a number of anatomically modern remains have been discovered in recent deposits in Africa. Included in this study are the crania from Fish Hoek (Keith, 1931) and Gamble's Cave 4 from Kenya (Leakey, 1935). Their morphology is essentially modern in all respects and they have been compared to the Bushman (Fish Hoek, Keith, 1931) and Nilotic Negroes (Gamble's cave, Rightmire, 1975).

The Gamble's cave 4 cranium has been dated at about 8000 years B.P. and the Fish Hoek cranium at 36000 +/− 2400 years B.P. on the basis of Carbon 14 (Oakley *et al.*, 1977).

Europe

Two groups of late Pleistocene hominids are well documented in Europe. The majority of specimens are representatives of *Homo sapiens* which show relatively modern morphology. The second group consists of material, particularly from western Europe, collectively known as "classic" Neanderthals.

Prior to the Neanderthals there is a relatively scant record of archaic *Homo*. Whether these remains represent archaic *Homo sapiens* or demonstrate a morphology derived in the direction of Neanderthals (and whether or not Neanderthals are ancestral to *Homo sapiens*) is a matter of debate (see later). For descriptive purposes I shall lump all of the European material into three groupings. The first I shall refer to as ante−Neanderthals (see Brauer, 1984 and Stringer and Andrews, 1988), the second as the ("classic") Neanderthals and the

third as anatomically modern *Homo sapiens*.

*(a) Ante–Neanderthals*

A number of fossils predate the "classic" Neanderthals. These include the Petralona cranium, from Greece (see previous section), cranial fragments from Arago, France, skull fragments from Swanscombe, England, and a damaged cranium from Steinheim, Germany (see Oakley *et al.*, 1971, Stringer *et al.*, 1984). Only the Steinheim cranium is included in this study.

*Cranial Morphology*

Their cranial morphology ranges from a pattern close to that of the representatives of archaic *Homo sapiens* from Africa (see earlier, e.g. Petralona–Brauer, 1984) to a mixture of plesiomorphous cranial characters and derived Neanderthal characters.

The Steinheim cranium has been dated as "Riss" or "Mindel–Riss" (Stringer *et al.*, 1984, >125,000 years B.P., Dennell, 1983). The face shows two non–Neanderthal characters – a canine fossa (Vandermeersch, 1978) and a flattened mid region (Stringer, 1978). The occipital is thin and rounded with a gracile torus. These apparently non–Neanderthal features can be set against the apparently derived Neanderthal–like nasal morphology and the presence of a suprainiac fossa (Hublin, 1978, Stringer *et al.*, 1984).

*(b) Neanderthals*

A number of definitions of the Neanderthals have been put forward. Hrdlicka (1930; 328) used a cultural definition: "the man and period of the Mousterian culture". Brace (1964) extended this to include an anatomical criterion: "the men of the Mousterian prior to the reduction in size and form of the Middle Pleistocene face". There are many problems in using a culturally derived definition not least of which is the difficulty in adequately defining the scope and boundaries of such traditions (see Mann and Trinkaus, 1973).

Brose and Wolpoff (1971) have defined the "Neanderthals" morphologically and temporally: "all hominid specimens dated within the time span from the end of Riss to the appearance of anatomically modern *H. sapiens* .... Neandertals evince crania expanded to modern size and posterior teeth reduced to modern size, along with anterior teeth and supporting facial architecture maintained in the very robust H. *erectus* condition". This is so broad as to encompass a very large range of material which is unlikely to be conspecific.

The term "Neanderthal" arose as a means of grouping together those specimens which shared a number of features with the Neander Valley Feldhofer cave fossil. As more and more discoveries have been made the term has been extended to a greater range of morphologies. This has led to the widespread usage of the term "classic" Neanderthals to refer to a more limited group of fossils which together exhibit a more restricted variability. They are concentrated towards the beginning of the last glacial period (80,000–40,000 years B.P., Mann and Trinkaus, 1973, but see Dennell, 1983 – ? double these dates).

From Europe a number of remains have been attributed to the "classic" Neanderthal group including, *inter alia*, those from the Neander valley, (Germany), La Chapelle-aux-Saints, La Ferrassie and Le Moustier (France), Monte Circeo, (Italy), and Gibraltar. Together these make up a large sample of European "classic" Neanderthals (see Mann and Trinkaus, 1973, Stringer *et al.*, 1984, Smith, 1984).

*Cranial morphology* (Stringer, *et al.*, 1984)

The morphology bears a superficial resemblance to that of the representatives of "early archaic *Homo sapiens*" which was described above. The reason for this is generally plesiomorphy. The Neanderthals are said to show derived (synapomorphous and autapomorphous) morphology in a number of features (Stringer *et al.*, 1984)

The Neanderthal cranial vault is long and low, the lambdoid region is flattened and there is occipital protrusion (Chignon or occipital bun). The cranial shape is spherical or oval in *norma occipitalis* ("en bombe"). There is a large occipito-mastoid crest relative to the size of the mastoid process, a supra-iniac fossa is present, and there is often an anterior mastoid tubercle. The external auditory meatus is positioned high relative to the root of the zygomatic process. There is a relatively large sphenoidal angle and the cranial base is flattened.

The midfacial region is prognathic and the nasal aperture is large with a lowered and sloping nasal floor. The maxilla and the double arched supraorbital

torus are extensively pneumatised. The dentition is positioned anteriorly such that there is a marked retromolar space and the mental foramen is usually under $M_1$.

*(c) Post–Neanderthal Homo sapiens*

Stringer *et al.* (1984) list a number of western European and Smith, (1984) lists central European fossil representatives of *Homo sapiens* which post date the Neanderthals and which show a relatively modern morphology.

*i. Western Europe*

From France a number of Upper Palaeolithic specimens are known. The fossils from Cro–Magnon (at least five individuals) show considerable variation in their supraciliary and occipital morphology. The face of Cro–Magnon 1 ("the old man") contrasts with the Neanderthal face in being relatively flattened but not in being positioned well forward of the middle portions of the vault (Stringer, *et al.*, 1984, Wolpoff, 1980b). The frontal is rounded. Frayer (1984) includes the Cro–Magnon remains in a Middle Upper Paleolithic group which he dates between 26 and 19 k.y. B.P. but the specimens may be older than this (Stringer *et al.* 1984)

The Chancelade skull, also from France, is dolichocephalic with a raised, keeled vault. The frontal region contrasts with that of the Cro–Magnon people in rising vertically and in having a less pronounced supraorbital relief. The face is long, broad and orthognathic with a narrow nasal aperture. This skull has been compared to that of modern Eskimos (Morant, 1926, Sollas, 1927) though the

resemblance is now considered to be superficial and of no evolutionary significance (Stringer, *et al.*, 1984).

From Britain a number of Upper Paleolithic and Mesolithic skeletal fossils have been recovered (see Oakley *et al.*, 1971, Stringer *et al.*, 1984). Included in this study is the cranium recovered from Gough's cave, Cheddar in 1877. and described by Seligman and Parsons (1914–15). These workers considered that the face is no more prognathic, and the vault no thicker than that of modern British crania. They do note, however that it is longer and deeper in the occipital region, that the orbits are wider and that there are minor differences in the frontal region. They conclude that overall "the cranium alone could not... be distinguished from that of a mediaeval Englishman". This view is consistent with the relatively recent dates attached to the cranium (approx. 9 k.y. b.p., Oakley *et al.*, 1971).

*ii. Central Europe*

The central European finds of early modern *Homo sapiens* have been discussed by Smith (1984). Examples which are included in this study are crania from the samples from Brno, Mladec and Predmosti in Czechoslovakia.

The Brno (Brunn) 3 cranium dates from 26–19 k.y. B.P. (Frayer, 1984). It has a distinctly modern appearance. The supra–orbital region is not developed into a pronounced ridge, the forehead is low and receding, the orbits are long low and slanting and the canine fossa is shallow. Matiegka (1929) concluded that the skull may be that of a female and that it resembles closely the Mladec 1

cranium.

The Mladec 1 cranium has a moderate upper facial height compared to other Upper Paleolithic specimens and a small facial breadth. The canine fossae are shallow and mid-facial prognathism is minimal (Wolpoff, 1980b). The supraorbital morphology is like that of modern Europeans. The cranium, which may be that of a female (Smith, 1984), dates from 33-26 k.y. B.P. (Frayer, 1984).

The Predmost 3 cranium is considered to be that of a male and is robust though its overall morphological pattern is clearly modern. Its brow ridges are well developed, its cranial vault is low and the face displays moderate prognathism (Smith, 1984). Frayer (1984) places it between 26 and 19 k.y. B.P.

## Asia & Australasia

### *i. Western Asia*

In a review of the fossil evidence for the recent evolution of *Homo sapiens* in western Asia, Trinkaus (1984) considered the Upper Pleistocene human remains to fall largely into four groups.

The oldest sample consists of the partial mandible from Azykh cave in the Lesser Caucasus, the "Galilee skull" from Mugharet el-Zuttiyeh and skeletal fragments from Tabun layer E, Israel, and remains from Mugharet el-Kebara

and Gesher Benot Ya'acov, Jordan. The youngest sample comprises anatomically modern humans from the Aurignacian of Mugharet el-Kebara and 'En-Gev I.

The middle two groups "abut the transition from archaic to anatomically modern humans" (Trinkaus, 1984). The older of these two groups resembles the Neanderthals of western Europe and includes the remains from Amud and Tabun layers C and D, Israel and Shanidar, Iraq (McCown and Keith, 1939, Suzuki and Takai, 1970, Trinkaus, 1983). The more modern sample includes the material from Djebel Kafzeh and Mugharet es-Skhul, Israel. The Skhul remains are estimated to date at about 40 k.y. B.P. whilst the dating of the Kafzeh sample has been more problematical with some authorities suggesting an age of about 90 k.y. B.P. and others favouring a date more in line with that of the Skhul material (see Trinkaus, 1984, Stringer, 1988).

The cranium of Skhul V from Mugharet es-Skhul is included in this study. Its morphology appears archaic in comparison to modern humans though its vault is high and rounded and the occipital region is full and rounded. Its calotte height index, zygomaxillary angle and relative mandibular size are similar to those of the peoples of the European Early Upper Paleolithic. It has a large robust face with a well developed supraorbital torus which is continuous over the glabella. Midfacial prognathism is less than that of European Neanderthals and Trinkaus (1984) concludes that the face is robust but otherwise anatomically modern.

*ii. The Far East*

The remains from Sambungmachan and Ngandong, Java and from Dali, China have been described earlier. It has also been noted that they differ from *Homo erectus* and may be representatives of archaic *Homo sapiens* (but see Wolpoff *et al.*, 1984).

More modern material from Java includes the remains from Wadjak (Oakley *et al.*, 1975). These specimens remain alone in the span between the Ngandong remains and the present in Java. They may be of a recent, perhaps Holocene date (Wolpoff *et al.*, 1984).

The cranium Wadjak 1 has been considered female (Oakley *et al.*, 1975). The cranial vault has been claimed to be thick and the lambdoidal region has been claimed to be flattened (Wolpoff *et al.*, 1984). There is an occipital hemi-bun and the frontal slope is comparable to that of modern Chinese crania. The supraciliary arches are only moderately developed and the nasal bones are flat. The midface is broad and the palate and mandible are robust. There is a degree of alveolar prognathism and an indistinct nasal margin. The zygomatic process of the maxilla forms a flat surface and there is a minimal canine fossa. Wolpoff *et al.* (1984) consider that the cranium reflects affinities to both Australoid and Chinese material.

*iii. Australia*

A number of anatomically modern remains have been discovered in Australia. They are variable in morphology and their dating is unclear (? >30 k.y. B.P.– present, see Stringer, in press).

Included in this study is the Keilor cranium (Wunderly, 1943) which Wolpoff *et al.*, (1984) consider to be similar to the Wadjak cranium described above. They note that this similarity is especially strong in the size, proportions and flatness of the face but that the Keilor fossil contrasts with the Wadjak cranium in possessing a weak angular torus, a greater glabellar prominence, smaller and more everted malars and in lacking an occipital hemi–bun. They suggest an age of about 13 k.y. B.P.

## B. Taxonomy and Phylogeny of Homo sapiens

The major current debate regarding the recent evolution of *Homo* concerns the relationship of the groups considered above and termed "archaic *Homo sapiens*", "pre–Neanderthals" and Neanderthals to the modern groups of *Homo sapiens sapiens*. At the extremes two models of recent human evolution can be distinguished, the "Neanderthal phase" and the "Noah's Ark" models (Howells, 1976).

The first, the "Neanderthal phase" model postulates a long period of independent evolution for the current geographic subgroups of mankind (Weidenreich, 1947, Coon, 1962, Brace, 1964, Radovcic, 1985). This model suggests that the current variation observable between modern racial groups has

its origin in the Middle Pleistocene. It requires that the evolution of each racial group occurred independently and in parallel from each of the more ancient stocks of *Homo* considered above.

The second, the "Noah's Ark" model postulates a single, relatively recent (Upper Pleistocene) origin for *Homo sapiens* with subsequent worldwide dispersal (Stringer, 1985, Stringer, *et al.*, 1984, Stringer and Andrews, 1988). This model attributes the current variability of *Homo sapiens* to the effects of recent geographic and cultural isolation. The more archaic (not anatomically modern) representatives of *Homo* are considered (save one – the founder population) to have been largely replaced by anatomically modern migrants.

A third view attempts to combine these two extremes by modifying the models to allow gene flow. In the "Noah's Ark" model interbreeding between modern migrants and pre-existing archaic groups can be invoked to explain apparent local continuities in the fossil record (Stringer *et al.*, 1984, Brauer, 1984). Whilst in the "Neanderthal phase" model interbreeding can be invoked to explain apparent discontinuities in the fossil record and the morphological similarity of modern populations.

It is clear from the work of several authors that the fossil record is equivocal. The European record in its western extreme shows evidence of morphological discontinuity between the Neanderthals and anatomically modern *Homo sapiens* (Stringer *et al.*, 1984) whilst the central and eastern European record seems to indicate a degree of morphological continuity (Smith, 1984). Smith (1984) and Stringer (in press) have noted that the central European

Neanderthals from Vindija and Sala show evidence of continuity with the robust but more anatomically modern specimens from Mladec and Predmost. Smith (1984) has concluded that "Neanderthals are reasonable candidates for the ancestral stock of modern Europeans".

A cladistic approach to the resolution of the questions surrounding the Middle and Upper Pleistocene evolution of *Homo* has recently been taken by several workers. The aim has been to determine which, if any, characters are present in an autapomorphous state within the "classic" group of Neanderthals and to see if the earlier "pre-Neanderthal" populations display any of these states or whether they make plausible common ancestors for modern and Neanderthal *Homo*.

Stringer(1985) in a study of the European Middle Pleistocene hominid fossil record discerns two groups, an older one comprising Mauer, Vertessollos, Bilzingsleben, Arago and Petralona fossils and a slightly younger one comprising, amongst others, the material from Swanscombe and Steinheim. In the older group he finds little evidence of exclusive synapomorphies with either Neanderthals or modern humans and in the younger group he finds evidence to align them with the Neanderthals. He aligns the archaic group with other material from Kabwe and Dali and suggests that "this group is morphologically close to an hypothesised morphotype for the common ancestor of Neanderthals and modern humans". Vandermeersch (1985) broadly agrees though he considers that the Arago and Petralona remains show a maxillary morphology which is more representative of the Neanderthals.

It is not only in Europe that apparent evidence of local continuity is found. Trinkaus (1984) in reviewing the fossil evidence relating to the archaic/modern human transition from western Asia demonstrates two phases of apparent morphological stasis. The first is the stasis of archaic morphology (Tabun E1, C2, Shanidar, Zuttiyeh, etc.) and the second is a period of stasis with gradual gracilization of the skeleton amongst more modern forms (Skhul, Quafzeh, 'En-Gev, etc). By contrast the transition (which Trinkaus places at about 40 k.y. B.P. and lasting about 5–10 k.y.) is associated with a complex process of anatomical alteration which occurred in a mosaic pattern differentially affecting the various skeletal regions. He takes this to suggest a significant elevation of interregional genetic exchange.

Wolpoff *et al.*, (1984) have reviewed the fossil evidence for the evolution of *Homo sapiens* in Asia. They indicate a number of similarities in cranial morphology, including facial flatness, frontal keeling, exostoses on the jaw bones, and incisor shovelling, between the fossils of *Homo erectus* from China and later *Homo sapiens* material. They conclude that the evidence "supports only one interpretation ....regional continuity".

The picture of regional continuity is also supported by the fossil evidence from Africa (Brauer, 1984). The difference lies, however, in the timing of the archaic/modern transition. Brauer indicates that there is a considerable body of evidence from eastern and southern Africa that anatomically modern humans originated in those regions in the Middle and/or early Upper Pleistocene and that this transition was complete some 100–70 k.y. B.P. This is considerably

earlier than the similar transition in other regions of the world. This leads Brauer to propose a phylogeny which is comparable to that hypothesised by Stringer (1985, see above). An isolated population of early archaic *Homo sapiens* (e.g. Arago, Petralona) in Europe developed into later Neanderthals whilst archaic *Homo sapiens* (Kabwe, Ndutu) in Africa developed into anatomically modern *Homo sapiens*. Later migration of the modern humans into the middle east and Europe resulted in replacement of the pre-existing populations. Brauer does not exclude the possibility of hybridisation.

Recently Stringer and Andrews (1988) have reviewed the modern genetic data and paleontological data concerning the origin of anatomical modernity in *Homo sapiens*. The genetic data (extant races) indicate low interpopulation diversity relative to intrapopulation divergences. There is a greater genetic diversity amongst sub-Saharan African populations relative to other human populations and this is taken to indicate a longer separation of populations within Africa than elsewhere. They consider that the paleontological evidence for an early appearance of modern humans in Africa and the Levant relative to other more peripheral areas and the late persistence of the Neanderthals in Europe is consistent with "a dispersal event from Africa by way of southwest Asia". It is concluded that although an "African origin for *Homo sapiens* is highly probable the exact time, place and mode of origin of the species cannot yet be determined".

## III . PREVIOUS MULTIVARIATE STUDIES OF CRANIAL FORM IN THE HOMINIDAE

Having reviewed the fossil evidence for the evolution of *Homo* and before proceeding to describe the multivariate study of the efficacy of different methods of cranial form description in certain fossil hominids it is appropriate to review previous multivariate morphometric studies. Some have concentrated on material from a limited time span (e.g. Howells, 1970, Bilsborough, 1972, Stringer, 1974a, 1974b, Clark, 1981, Brauer, 1984, van Vark, 1984, Brauer and Leakey, 1986, Bilsborough and Wood, 1988) whilst others have considered material from a broader time span (e.g., Boyce, 1969, Bilsborough, 1973, 1984, O'Higgins and Williams, 1987).

I shall review these studies according to this arbitrary subdivision beginning with studies of early hominid cranial morphology.

Bilsborough and Wood (1988) have undertaken an extensive study of hominid cranial diversity in which they have studied a wide range of material. They concentrated on Pliocene and early Pleistocene material and have, to date, reported the results relating to facial diversity. The facial region was described by 24 variables of which 20 were submitted to multivariate analysis. The multivariate analysis is based on generalised distances and Q−mode canonical variate analysis based on a correlation matrix. They concluded from the univariate analysis of their data that there is marked variation in gross facial dimensions within early hominids due, at least in part, to variation in cranial size. *A. boisei* specimens have faces that are substantially longer and broader

than those of *A. africanus* and their malar regions are absolutely and relatively deeper. Only KNM-ER 1470 "comes near to matching the 'robust' australopithecines in malar development" and facial breadth. The multivariate analysis demonstrates that "both *Australopithecus* and *Homo* encompass comparable ranges of diversity in facial proportions" and that the maximum difference is between recent humans and the "robust" australopithecines. *A. africanus* is equidistant from *H. habilis* and other smaller Lower Pleistocene remains on the one hand and *A. robustus* on the other. KNM-ER 1470 is relatively isolated but its nearest neighbours include the "robust" australopithecines. Its "facial pattern is basically hominine, but ... in some respects mimics that of robust australopithecines". They state that, overall, the results indicate two broad patterns of facial proportions within hominids. One is characteristic of early hominids with opposite extremes within this group represented by *A. boisei* and *H. habilis*. The other typifies hominids from the later Lower Pleistocene onwards, ranging from early "*erectus*" (KNM-ER 3733), with its relatively tall and narrow face, to later *Homo*.

Clark (1981) has carried out a multivariate analysis of 8 craniofacial dimensions and indices in order to assess the phenetic affinities of the SK 847 composite cranium and the SK 15 and SK 45 mandibles (see earlier - *?Homo habilis*). He statistically compared this cranium to representatives of "robust" (South and East African) and "gracile" (South African) australopithecines and "*Homo erectus*" (Asian and African). He performed a step-wise discriminant analysis in order to define a set of variables giving maximum between-group

discrimination and calculated Mahalanobis' distances. The results of his analysis suggested that the composite cranium is most similar to the South African "gracile" australopithecines whilst the SK 15 and SK 45 mandibles are most similar to his group of "*Homo erectus*". He concludes that this study raises the possibility that the cranium and mandibles (esp. SK 15) are not conspecific, alternatively if SK 847 and SK 45 are conspecific there is evidence of mosaic evolution.

Brauer's (1984) approach to multivariate analysis differs from the previous two studies. He undertook principal component analyses (instead of canonical/discriminant analyses) of dimensions taken from restricted anatomical regions (frontal, parietal, upper facial) of representatives of archaic *Homo sapiens*. He concluded from these analyses and from a number of comparative anatomical approaches that he could classify the African finds which he studied into a number of grades: *Homo sapiens* "grade 1" (early archaic) which includes amongst others Kabwe 1, Ndutu and Bodo, *Homo sapiens* "grade 2" (late archaic) including Florisbad, Omo 2, Laetoli 18, *Homo sapiens* "grade 2a" (Neanderthaloids – resembling Neanderthals) including Jebel Irhoud and Mugharet el'Aliya, and *Homo sapiens* "grade 3" (anatomically modern). The representatives of "grade 1" could be subdivided into northwestern, eastern and southern groups. He considers "grade 2" to represent a spectrum of morphology ranging from those which evolved from parts of the early archaic spectrum to those which resulted from hybridisation with anatomically modern humans ("grade 3"). He states that "it appears likely that the North African Neanderthaloids

(*Homo sapiens* "grade 2a") developed out of the spectrum of the pre-Neanderthals and near eastern Neanderthals". This leads him to propose the phylogeny discussed earlier in which an isolated population of early archaic *Homo sapiens* (e.g. Arago, Petralona) in Europe developed into later Neanderthals whilst archaic *Homo sapiens* (Kabwe, Ndutu) in Africa developed into anatomically modern *Homo sapiens*.

Brauer has further investigated the African fossil record of archaic *Homo sapiens* together with R.E. Leakey in a multivariate study of the Eliye Springs cranium, ES-11693 (Brauer and Leakey, 1986). He again performed principal component analyses based upon regional sets of variables. The authors conclude that the cranium has closest affinities to the "late archaic *Homo sapiens*" ("grade 2") material defined in Brauer's earlier study.

Van Vark (1984) has undertaken a multivariate analysis of form in a number of Middle to Late Pleistocene crania. He calculated the Mahalanobis' distances between the fossil material on the basis of a pooled variance covariance matrix from a large sample of modern human crania. He estimated missing values for damaged crania by multiple regression. His results indicate that the Broken Hill (Kabwe), Petralona and Steinheim crania "while mutually being relatively close, are very distinct from all other skulls" (anatomically modern humans, Neanderthals, Solo and Asiatic *Homo erectus*). Furthermore, Asiatic *Homo erectus* is, in this study, closer to recent man than are Petralona, Steinheim or the Broken Hill skull. This result led van Vark to conclude that since the circa 1 million year old "Pithecanthropus 2" "seems less different from

recent skulls than the skulls of Broken Hill, Petralona and Steinheim, it seems likely ...that the two separate lineages were already in existence at that time".

Stringer (1974a), calculated Mahalanobis' $D^2$, canonical variates and dendrograms from variable sets taken from localised and more general anatomical regions of a number of crania of later Pleistocene hominids. He found several consistent trends in the analyses: a relatively large distance between "classic" European Neanderthals and anatomically modern populations; middle eastern Neanderthal-like crania (e.g. Tabun) whilst being similar to the "classic" group were closer to modern forms; and Skhul V and Omo 1 were always closer to modern crania than to the "classic" Neanderthals. The finding of a difference between the Tabun remains and Skhul V in their affinities for modern populations and Neanderthals is consistent with the outcome of a multivariate study undertaken by Howells (1970).

Stringer (1974a) considered that the results cast doubt on the possibility of a close relationship between the "classic" Neanderthals and his Upper Paleolithic sample. He discerned differences in regional morphology between the "classic" Neanderthals and more anatomically modern forms. These included a larger nasio-occipital length, a narrower upper face and a high degree of mid-facial projection. The study indicated that the Broken Hill cranium approximated the Neanderthals in general vault form though the cranium is narrower, has a larger lambda-opisthion subtense, possesses a lower, longer and narrower frontal with larger supraorbital projection and is more like modern forms in parietal dimensions. Facially the Broken Hill skull exhibited a generally similar facial

morphology to that of the cranium from Petralona. Comparison of the generalised distances between the Broken Hill cranium and recent populations from a wide geographic distribution "provided no support whatever for a polyphyletic scheme of human evolution".

Lestrel (1974), has employed Fourier analysis (see chapter 2) of the midline projection of the cranial vault of a limited sample of fossil hominoid crania in order to examine the applicability of this technique. He has demonstrated that canonical analysis of the Fourier coefficients is plausible and that size influences, which swamp morphological influences, in the accompanying analysis can be usefully reduced by scaling the data for the magnitude of the first cosine component ($a_0$ – see chapter 2).

Bilsborough has undertaken extensive studies of the cranial morphology of a wide range of fossil hominids (Bilsborough, 1972, 1973, 1984, and see above) concentrating on their phenetic affinities whilst Boyce (1969) has studied a wide range of fossil hominid crania in order to compare the multivariate approaches available at that time.

Bilsborough (1973) calculated rates of morphological change between groups based upon Mahalanobis' distances calculated from cranial vault dimensions and elapsed time between the appearance of various taxa. He showed that during the Lower Pleistocene there were considerable changes in cranial vault morphology though these differences were occurring more slowly than those encountered in the Middle Pleistocene. The Upper Pleistocene has seen a reproportioning of the vault with the development of considerable morphological

diversity and little change in gross capacity.

In a later study (Bilsborough, 1984) he employed a number of newer multivariate techniques in addition to the calculation of Mahalanobis' distances in a study of morphological change in cranial proportions during hominid evolution. These include a technique (which he calls phyletic scaling) for comparing morphological change within one grouping of taxa with that encountered in another and Generalised Procrustes Analysis which he uses in order to integrate the results of his different regional analyses.

His matrix of Mahalanobis' distances indicates that there are similarities between *A. africanus*, Olduvai *H. habilis* and KNM–ER 1813 though the australopithecines differ in having less orthognathic faces and less retracted zygomatic processes. The "robust" australopithecines are widely divergent from these "gracile" forms and from later *Homo*, especially in those regions involved in masticatory activity. Early *Homo* differs from *Homo erectus* particularly in the upper face in having a less pronounced supraorbital torus and smaller breadths. He notes that "early *Homo erectus*" is widely separated from later "*erectus*" but feels that this can be accounted for by an ancestor–descendant sequence rather than two lineages. Bilsborough used the distance between Neanderthals and modern men to assess the significance of the differences encountered between other groupings of crania. He considers that KNM–ER 1813 is very similar to *Homo habilis* (Olduvai) and may be conspecific. This group is, in turn, very different from "early *Homo erectus*". KNM–ER 1470 is distinctive, it resembles *Homo erectus* in neurocranial features but diverges widely in facial proportions.

Bilsborough employed generalised procrustes analysis to rotate, translate and scale the results from the analysis of each region so that the distance of each region from the group centroid was minimal relative to the distances between group centroids. Effectively this results in an appreciation of the morphological interaction of the various regions. In his study most cranial regions regularly clustered about each centroid indicating a high degree of morphological and functional integration. The exception was the complex of measurements relating to head balancing, probably because of a primary association with locomotor habitus. The relative positions of the centroids indicate "average" differences between groups and in this study they conformed to the broad consensus of their morphological relationships. The distinctiveness of *A. boisei* was emphasised and *A. africanus* was shown to differ from *H. habilis* which was similar to early *H. erectus*. Early *H. erectus* was markedly separated from later *H. erectus* and there was a tight clustering of Middle and Upper Pleistocene remains.

## Summary

From this brief review of multivariate studies of cranial form in fossil hominids it is clear that a number of approaches have been adopted. The commonest is to calculate Mahalanobis' distances from a selected set of angles and linear dimensions and to derive canonical variates from the resultant D matrix by Gower's (1966) Q-technique. Brauer has, however, preferred to use principal components analysis, presumably because of the difficulty of estimating

a pooled within group variance–covariance matrix which is applicable to fossil (of which there may only be one known representative) as well as living species.

Generally the outcome of phenetic studies of the cranial morphology of fossil hominids is in agreement with the broad view of morphological relationships, though there are a number disagreements between the studies of different workers (e.g. Stringer, 1974a and van Vark, 1984, and see later). The studies have mainly served to confirm earlier subjective assessments but they have occasionally undermined previous viewpoints (e.g. the degree of similarity between early Neanderthal–like populations and later modern populations in different geographic regions, see Brauer, 1984, Howells, 1970, Stringer, 1974a). Bilsborough (1984) has indicated that multivariate studies can lead to new types of information, namely assessments of morphological/functional integration. The main contribution of multivariate studies has, however, been the clarification and quantification of patterns of morphological similarity either between whole crania or between more limited morphological regions.

Lestrel (1974) has shown the feasibility of using Fourier analysis to obtain a detailed description of regional cranial morphology and has further shown that the coefficients of the Fourier series can be usefully submitted to canonical analysis. A more recent Fourier analytic study of the cranial morphology of a number of living and fossil Primate species has been undertaken by O'Higgins and Williams (1987) who demonstrated that this technique allows the possibility of relatively automated data collection and have indicated that the outcome of

studies based on Fourier coefficients calculated from the cranium is concordant with a broad consensus view of hominid cranial morphological relationships. There has been no formal comparison of Fourier and other descriptive techniques in hominid phenetics.

# IV. A STUDY TO COMPARE DIFFERENCES IN THE PATTERNS OF CRANIAL VARIATION OBSERVED BETWEEN CERTAIN GROUPS OF FOSSIL HOMINOIDS USING FOURIER ANALYSIS AND LINEAR AND ANGULAR MEASUREMENTS.

## INTRODUCTION

This third study has been designed to investigate the differences in patterns of variation of cranial form which are observed between certain groups of fossil hominids when different methods are used to describe cranial morphology.

The background to the study of much of this material has been outlined earlier in this chapter. The studies of chapter 2 have indicated a high degree of concordance between the patterns of phenetic relationships demonstrated by a number of means. However, the comparisons of methods were based upon studies of apes and humans and may have been misleading because common to each distance matrix were large and small distances but few of intermediate size (this follows from the fact that there are large morphological differences, and therefore taxonomic distances, between ape and human OTUs but within apes and men the distances are small) – see Fig. 2.19. The high correlations which were noted between the distance matrices calculated from different data may well have been heavily influenced by this pattern of differences such that they suggested a higher degree of correspondence than would have been the case had there been available a sample of crania of "intermediate" morphology.

The studies of chapter 3 contrast with those of chapter 2 in suggesting that analyses of Fourier data may not agree very well with the outcome of studies of linear and angular measurements. This difference in result reflects the fact that Fourier data, in contrast to homology dependent mesurements, give equal weight to all outline points.

The presence of a hominid fossil record provides a potentially useful subject for the further investigation of the conflict in outcomes. In chapter 2 the groups which were compared show either a relatively large or a relatively small difference in cranial morphology. In chapter 3, however, the differences in within-group cranial morphology are far less. In this chapter a "spectrum" of hominoid cranial morphologies will be examined including an ape species, a race of modern humans and a number of fossil hominids.

The study comprises a number of canonical analyses which are based upon linear and angular measurements and Fourier coefficients. Principal components analysis allows, to some extent, the assessment of between group relationships. There are, however, two major disadvantages. First, the PCs are calculated so as to best summarise the phenetic differences between all individuals. As the number of individuals increases so the number of PCs needed to obtain a good summary of the data increases and interpretation becomes difficult. Second, PCA re-expresses the positions of individuals on a series of axes which are uncorrelated between individuals.

Canonical analysis expresses the positions of group centroids on a series of axes which are uncorrelated between groups and which are directed to the

summary of between group relations. It is a discriminant technique and as such leads to a more concise description of between group differences than does PCA (see appendix B).

The results of studies based on one set of data are compared with those from the other. The comparison takes account of the findings of previous workers who have examined the cranial morphologies of fossil hominids.

The study of fossil material presents some new problems. Many crania are fragmentary and have been reconstructed, in addition this study relies upon measurements taken from casts which adds another source of error. A further problem arises because of the nature of the fossil record; no species can be unequivocally defined and the extent of overlap of variation between taxa and of variability within taxa is unclear (see the earlier review). It has therefore been important to investigate the degree of error introduced by the use of casts and the need to estimate data and to study patterns of variation within the hominid fossil record. The study described below investigates these issues in addition to comparing the utility of different methods of shape description in studies of hominid cranial morphology.

# MATERIALS AND METHODS

## MATERIALS

### Modern

The skulls of chimpanzees and negroids described in chapter 2 (table 2.1) were used to provide reference populations for the study of fossil cranial casts.

### Fossil

The fossil casts used in this study are listed in table 4.1. They include ten fossils from the relatively recent history of *Homo* which are generally complete and which are all assigned to *Homo sapiens* by most authorities. Six of these fossils are from Europe, two from Africa (Gamble's cave and Fish Hoek), one from Java (Wadjak 1) and one is from Australia (Keilor).

The study includes eight fossil crania which occupy the record of human origins between the time of *Homo erectus* grade hominids and the emergence of modern *Homo sapiens* in Europe. Five of these are commonly included in the "classic" western European Neanderthal group: Gibraltar I, La Chapelle-aux-Saints I, La Ferrassie I, Monte Circeo I and Le Moustier I. The specimen from Le Moustier is believed to be that of an adolescent. Two of the remaining crania have been compared with the Neanderthals, – viz. Skhul V from Israel and the Kabwe I cranium from Zambia; the third is the Steinheim cranium from Germany.

Three fossils usually assigned to *Homo erectus* are included. The wide geographical distribution of this grade (see earlier) is reflected by these specimens. The cranium from East Turkana, Kenya, KNM-ER 3733 is the

oldest representative. Two heavily reconstructed specimens represent the far eastern varieties, a composite reconstruction of *"Sinanthropus"* made by Weidenreich and Swan (Weidenreich, 1937) and Weidenreich's (1941a) reconstruction of a Javanese cranium *("Pithecanthropus")* based upon a recovered calvaria, maxilla and some teeth (Sangiran 4).

The remaining material consists of African fossils which have been assigned to either *"Paranthropus"*, *Australopithecus* or early *Homo*. All of this material is discussed and described earlier. It includes, from East Africa, OH 5, KNM–ER 406, OH 24, KNM–ER 1470 and, from South Africa, Sts 5.

TABLE 4.1

Provenance of fossil Skull casts

| Group | Collection | Museum Name and Number | | Abbrev. |
|---|---|---|---|---|
| Fossil *Homo sapiens* | BMNH (P) | Cro-Magnon 1 | EM-1795 | Cro-M. |
| | BMNH (P) | Gough's Cave 1 (Cheddar) | M 16961 | Gough. |
| | BMNH (P) | Chancelade 1 | M 16689 | Chanc. |
| | BMNH (P) | Predmost 3 | M 16630 | Predm. |
| | BMNH (P) | Brno (Brunn) 3 | EM-266/7 | Brno. |
| | BMNH (P) | Mladec 1 | EM-1213 | Mlade. |
| | BUA | Gamble's Cave 4 | - | Gambl. |
| | BUA | Fish Hock 1 | - | Fish. |
| | BUA | Wadjak 1 | - | Wadja. |
| | BUA | Keilor 1 | EM-235 | Keilo. |
| Neanderthals and other late fossils | BUA | Gibraltar 1 | - | Gibra. |
| | BMNH (P) | La Chapelle-aux-Saints 1 | EM-1792/3 | Chap. |
| | BMNH (P) | La Ferrassie 1 | M 16847 | Ferra. |
| | BMNH (P) | Monte Circeo 1 | EM-273 | Circe. |
| | BUA | Le Moustier 1 | - | Moust. |
| | BMNH (P) | Es-Skhul V | - | Es Sk. |
| | LUA | Kabwe (Broken Hill) 1 | - | Kabwe. |
| | BMNH (P) | Steinheim 1 | EM-1777 | Stein. |

| *Group* | *Collection* | *Museum Name and Number* | | *Abbrev.* |
|---|---|---|---|---|
| *Homo erectus* grade fossils | BMNH (P) | Sangiran 4 (recons) (Weidenreich 1941a) | EM – 1811 | Sangi. |
| | BMNH (P) | *"Sinanthropus"* (recons) Weidenreich (1937) | M 15725 | Sinan. |
| | BMNH (P) | KNM – ER 3733 | EM – 2096 | 3733 |
| Australopithecines and early *Homo* | BMNH (P) | OH 5 | EM – 1317/8 | OH5 |
| | BMNH (P) | KNM – ER 406 | EM – 1613 | ER406 |
| | BMNH (P) | OH 24 | EM – 1388 | OH24 |
| | BMNH (P) | KNM – ER 1470 | – | 1470 |
| | BMNH (P) | Sts 5 | M16861 | Sts5 |

BMNH (P) = British Museum (Natural History), Dept of Palaeontology
BUA = Birmingham University, Dept of Anatomy
LUA = Leeds University, Dept of Anatomy

## METHODS

### i. Measurement methods

The measurements from the extant and fossil material included a subset (34) of the cranial linear and angular dimensions used in the studies of chapters 2 and 3 (tables 2.2, 2.3 and 4.2). A further subset of the 25 dimensions and angles taken from the midline craniogram (see chapter 2) was also prepared in order to allow a comparison with the (midline) Fourier data.

The square root of the area of the mid-sagittal projection of each cranium was recorded for use as a size measure (see chapter 2).

The sine-cosine Fourier coefficients calculated from each modern cranium were made available for this study. The method of measurement and calculation of these variables is discussed in chapter 2.

The midsagittal tracing of each fossil cast was reconstructed where necessary (appendix A) and used to calculate Fourier coefficients by the same method as was applied to the crania of living species. In the case of the analyses based upon Fourier data KNM-ER 3733 was omitted from the group of *Homo erectus*.

It is appropriate to consider here the particular problems associated with the measurement and description of the fossil material:

## TABLE 4.2

**Linear and angular dimensions taken from all Casts of Fossil crania**

Neurocranium

1 Maximum length
2 Maximum breadth
3 Basi-bregmatic height
4 Auricular height
5 Postorbital breadth
6 Frontal height
7 Frontal chord
8 Parietal height
9 Parietal chord
10 Occipital height
11 Occipital chord
12 Foramen magnum length
13 Foramen magnum breadth
14 Angle b-l-o
15 Angle l-o-ba

Viscerocranium

16 Upper facial height
17 Palatal length
18 Palatal breadth
19 Nasal breadth
20 Nasal height
21 Subnasal height
22 Orbital height
23 Orbital breadth
24 Infraorbital breadth
25 Bizygomatic breadth

Viscerocranial-Neurocranial relationships

26 Basi-infraorbital length
27 Basi-nasal length
28 Basi-prosthion length
29 Basi-staphylion length
30 Angle ba-n-b
31 Angle ba-n-pr
32 Angle n-b-l
33 Angle n-ba-pr
34 Angle o-ba-n

a) Problems of preservation and reconstruction

A substantial number of the casts of fossil material included in this study were fragmentary or reconstructed. It was necessary, therefore, to estimate certain of the dimensions required for the analyses. The options available for these estimations included visual approaches based upon anatomical experience and the general contours of the surviving portions and statistical estimations designed to derive values which did not alter the mean and variance of the populations to which the damaged remains belong. The problem with the statistical approach is that it depends on prior knowledge of population membership, a situation which does not exist for much of the material, or on the assumption, which is unproven, that crania from different populations behave the same way in terms of functional–morphological integration.

It was decided to adopt the admittedly subjective approach of estimation by visual means based upon anatomical experience and knowledge. The data were initially collected by the late Professor E.H. Ashton and by Professor W.J. Moore. I later re–examined each of the fossil casts used in this study and checked each of the estimated and unestimated dimensions and angles for accuracy and reliability. The data, together with an account of the problems of estimation of each value are presented in Appendix A.

b) Problems associated with using casts

A large proportion of the original fossils are fragmented and have been reconstructed to some degree. These reconstructions while not the ideal material

for biometric or visual study are, all that is available. The processes of fossilisation, cleaning and reconstruction all introduce error.

It is frequently argued that the use of casts of these restored specimens or of unmodified original specimens introduces a large and unwarranted source of error (e.g. Stringer, 1986). The examination of originals was not practicable for most of the material and, in any case, the principal aim of this study was to compare the utility of different shape measurement methods. If the results are to be taken to indicate anything of relevance to the taxonomy of the fossil material, however, it becomes imperative to consider the degree of error that is introduced by the use of casts. If it is large the cast should be discarded.

It is of no use to examine the distortion in a single cast and to extrapolate from this to all casts: each cast was made in different conditions, at different times and by different people. The only appropriate test is to compare the dimensions taken from each cast with those that have been published in the literature and which were taken according to the same criteria as the dimensions in this study. This raises a problem; not all dimensions which have been taken from the original and have been published are compatible with those taken in this study.

A comparison was undertaken of those measurements from the original material (or original reconstruction) which could be traced in the literature with their counterparts, taken for this study, from casts. The number of measurements which were comparable and could be traced for each specimen was small, only 3 or 4 on average (10%). They do, however, allow an assessment of the degree

of shrinkage over large regions (e.g. cranial length) and the combination of two or more variables allows distortion to be examined. For each variable its counterpart from the fossil was used to calculate a percentage difference between the fossil and cast as follows:

$$\% \text{ difference} = (\text{Fossil dim.} - \text{cast dim.}) * 100 / \text{Fossil dim.}$$

The absolute value of this quantity was averaged over all available comparisons on each fossil. A note was made of whether the fossil was larger than the cast in each variable. Table 4.3 presents the results of this enquiry. The number of dimensions which were available from the original is listed, together with the source reference, the average % difference between the fossil and the cast and a note of the relative size of fossil and cast in the available dimensions.

The results presented in table 4.3 allow considerable confidence to be placed on the accuracy of the casts. In general the difference between fossil and cast is of the order of 1%–2%. The results further indicate that the fossil dimensions are smaller than those from the cast as often as they are larger: there is no evidence of generalised shrinkage. The degree of error which is encountered is about that which would result from measurement error. This is reflected in the extent to which authorities disagree over certain dimensions taken from originals (Day, 1986, also lists large disagreements in dimensions taken from originals – up to 9% for Steinheim).

## TABLE 43

### The Accuracy of Fossil Casts used in this study

| FOSSIL | Number of original dims located in refs. | Average % difference (f−c)/f % | Fossil bigger + smaller − or same 0 | Source refs. |
|---|---|---|---|---|
| Cro-Magnon 1 | 4 | 2.31 | −/0 | 3,6 |
| Gough's Cave 1 | 4 | 5.3 | −/+ | 20 |
| Chancelade 1 | 3 | 1.56 | − | 15 |
| Predmost 3 | 7 | 1.19 | −/0/+ | 18 |
| Brno 3 | 6 | 1.96 | +/− | 13 |
| Mladec 1 | 7 | 2.35 | −/0/+ | 18 |
| Gamble's Cave 4 | 5 | 0.49 | +/− | 9 |
| Fish Hock 1 | 6 | 1.13 | −/0 | 8 |
| Wadjak 1 | 2 | 2.22 | − | 5 |
| Keilor 1 | 3 | 2.91 | −/+ | 23 |
| Gibraltar 1 | 4 | 4.41 | +/0/− | 1,4,14 |
| La Chapelle 1 | 5 | 2.08 | +/− | 1,2,14 |
| La Ferrassie 1 | 2 | 1.40 | − | 6 |
| Monte Circeo 1 | 1 | 0.00 | 0 | 21 |
| Le Moustier 1 | 3 | 0.69 | + | 14,16,17 |
| es-Skhul V | 5 | 1.92 | −/+ | 14 |
| Kabwe 1 | 5 | 1.28 | −/0 | 6,14,17,19 |
| Steinheim 1 | 2 | 0.79 | − | 6 |
| Sangiran 4 | 2 | 0.56 | +/− | 6 |
| "*Sinanthropus*" | 2 | mid range of vars in:− | | 5 |
| KNM-ER 37333 | 5.8/4.32* | | +/− | 12 |
| OH 5 | 7 | 3.39 | +/− | 22 |
| KNM-ER 406 | 4 | 0.55 | − | 11 |
| OH 24 | 4 | 0.43 | −/0 | 10 |
| KNM-ER 1470** | 4 | 2.64 | −/+ | 7 |
| Sts 5 | 2 | 1.26 | − | 6 |

* depending on def. of prosthion ** intermediate recon.

REFERENCES:


1 Boule, 1911a
2 Boule, 1911b
3 Broca, 1868
4 Busk, 1869
5 Day, 1977
6 Day, 1986
7 Day, Leakey, Walker and Wood, 1974
8 Keith, 1931
9 Leakey, 1935
10 Leakey, Clarke and Leakey, 1971
11 Leakey, Mungai and Walker, 1971
12 Leakey and Walker, 1976
13 Matiegka, 1929
14 McCown and Keith, 1939
15 Morant, 1926
16 Morant, 1927
17 Morant, 1928
18 Morant, 1930
19 Pycraft, 1928
20 Seligman and Parsons, 1914/15
21 Sergi, 1948
22 Tobias, 1967
23 Wunderly, 1943

There are a few casts with which there appear to be problems of dimensional stability. The Gough's cave 1 cast differs on average 5.3 % from the fossil. However because of damage to the face seventy five percent of the available measurements were estimates. It is not surprising therefore that the estimates differ to this degree. In the non-estimated cranial length, the cast and original differed by only 0.5%.

The Gibraltar 1 cast shows an average error of 4.4 %. No clear cause for this can be found. It must be assumed that it is the result of inter-observer error and cast distortion.

The cast of KNM-ER 3733 differed on average 5.8% from the original. This figure may well be inflated because of differences in the way in which the position of prosthion was estimated. The tracing shows that the maxilla extends a little way in front of the point indicated by the junction of the incisors. The dimensions from the cast used in the present study were based upon the latter point. It is unclear (Leakey and Walker, 1976) whether the most anterior point of the maxilla was used in the quoted original dimension. Adjustment of the cast dimension for comparison reduces the average error to 4.32 %. The other dimension which differs is cranial breadth. There is room for inter-observer error in the determination of this variable, added to which the braincase is fragmented. These considerations aside it seems that interpretation of the results derived from this cranium should allow for about a 5% error in the measurements.

A smaller error, of about 3.4% is present in those variables compared between the OH 5 cast and fossil. This value may be inflated by the fact that crests were ignored in this study in the estimation of cranial length while it is unclear if this was the case in Tobias's study (1967). If the crest is included in the cast dimension the error becomes less than 3%.

From this enquiry it seems that errors introduced by the examination of casts of fossil material in this study are minimal, they are generally about 2% and never appreciably above 5%.

ii. Statistical methods

The primary aim of this study is to examine the differences in result that are obtained by study of linear and angular dimensions and Fourier coefficients. The casts of fossils include a number of reconstructed regions and several dimensions have been estimated, consequently the robusticity of Fourier analysis to such reconstruction can be assessed. A subsidiary, but still important aim is to consider the significance of the phenetic relationships of the fossil crania in the light of previous studies.

The OTUs used in these phenetic studies were determined from a study of the literature and by a number of multivariate analyses directed towards ensuring homogeneity and equality of variance of fossil groups. The studies which led to the use of these OTUs are presented in appendix B. and the OTUs that were identified are:

1. Representatives of anatomically modern (a.m.) *Homo sapiens*
2. Skhul V
3. "classic" European Neanderthals
4. Kabwe 1
5. Steinheim
6. Representatives of the grade *Homo erectus*
7. *A. boisei*
8. KNM-ER 1470
9. Sts 5
10. OH 24

Between-OTU phenetic relationships were assessed by canonical analysis of: the first 20 pairs of sine-cosine Fourier coefficients, the 30 sine-cosine Fourier components which performed best in discriminating between the modern groups (see chapter 2), 25 scaled and 34 scaled (against square root of area of midline area, angles were not altered) variables (chapter 2 and table 4.2). In preliminary tests the results of studies using angles and scaled dimensions were found to differ very little from those which used raw variables. Scaled variables were, however, used for the studies of this chapter in order to be consistent with the analyses of (scaled) Fourier coefficients and to reduce any size influence on observed phenetic relations. The dimensions and angles were logged in order to equalise within group variances and the Fourier coefficients were not (see chapter 2). All analyses were undertaken using SAS (1982) and NTSYS-PC (Rohlf,

1987).

Plots of the scores of groups on the first few canonical axes were prepared for each analysis. The number of axes to be used in these plots was selected such that approximately 95% of the total between group variance was described. The correlations of the size of individuals with their scores on each canonical axis were determined and matrices of between group Mahalanobis' distances were calculated.

The matrices were compared by :

1. calculating correlations between them
2. calculating a matrix of percentage differences in relative Mahalanobis' distances derived from Fourier data and 25 scaled dimensions; this matrix was produced by scaling each matrix to have the same *Pan* – negro distance and then calculating the percentage difference between each distance ((25 midline – Fourier)*100/25 midline)
3. computing UPGMA phenograms and cophenetic correlations from each Mahalanobis' distance matrix.

## RESULTS

### I. Comparison of the patterns of similarity and difference between fossil and modern groups demonstrated by study of midline linear and angular measurements versus 3-dimensional measurements.

The study of chapter 2 suggested that the pattern of phenetic relationships demonstrated by the midline data differed little from that resulting from the study of midline plus off-midline data.

The Mahalanobis' distance matrix calculated from 34 angles and dimensions (table 4.2) in this study is presented in table 4.4 and that from 25 midline and projected midline variables in table 4.5. The correlation between these two matrices is 0.94 ($P<0.001$), indicating a high degree of concordance.

**TABLE 4.4**

Mahalanobis' distance matrix calculated from 34 scaled dimensions and angles

| | boi | Pan | erec | a.m. | Kabw | Nean | Negr | Olt24 | SkhV | Stei | Sts5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A.boisei | | | | | | | | | | | |
| Pan | 13.70 | | | | | | | | | | |
| H.erectus | 19.64 | 21.39 | | | | | | | | | |
| a.m. H.sapiens | 24.48 | 26.40 | 12.34 | | | | | | | | |
| Kabwe | 21.62 | 23.74 | 11.03 | 9.91 | | | | | | | |
| Neanderthals | 22.49 | 23.97 | 7.78 | 9.25 | 10.09 | | | | | | |
| Negroes | 22.04 | 23.12 | 12.39 | 5.23 | 10.60 | 10.34 | | | | | |
| Olt 24 | 21.63 | 20.01 | 17.20 | 17.59 | 18.06 | 19.18 | 15.06 | | | | |
| Skhul V | 22.93 | 24.68 | 12.08 | 7.70 | 10.86 | 11.05 | 7.61 | 15.49 | | | |
| Steinheim | 22.87 | 21.85 | 11.13 | 12.65 | 14.31 | 11.39 | 11.86 | 15.45 | 11.42 | | |
| Sts 5 | 11.72 | 11.10 | 19.88 | 23.62 | 21.29 | 22.45 | 20.45 | 17.10 | 21.37 | 20.35 | |
| KNM-ER 1470 | 13.07 | 15.51 | 15.61 | 19.21 | 16.24 | 17.32 | 17.26 | 19.71 | 18.96 | 18.05 | 14.94 |

## TABLE 45

**Mahalanobis' distance matrix calculated from 25 midline dimensions and angles**

| | boi | Pan | erec | a.m. | Kabw | Mean | Negr | OH24 | SkhV | Stei | Sts5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A.boisei | | | | | | | | | | | |
| Pan | 9.30 | | | | | | | | | | |
| H.erectus | 12.19 | 16.49 | | | | | | | | | |
| a.m. H.sapiens | 16.05 | 20.81 | 9.29 | | | | | | | | |
| Kabwe | 15.11 | 20.16 | 7.61 | 7.25 | | | | | | | |
| Neanderthals | 13.62 | 18.96 | 6.10 | 6.39 | 5.80 | | | | | | |
| Negroes | 14.95 | 19.08 | 9.95 | 3.90 | 9.08 | 7.95 | | | | | |
| OH 24 | 15.45 | 15.70 | 15.32 | 15.87 | 17.47 | 16.94 | 13.98 | | | | |
| Skhul V | 14.98 | 19.23 | 9.14 | 5.86 | 8.31 | 7.82 | 6.08 | 13.99 | | | |
| Steinheim | 15.79 | 17.27 | 9.18 | 10.40 | 10.86 | 10.04 | 10.36 | 13.38 | 8.59 | | |
| Sts 5 | 9.19 | 8.49 | 15.45 | 18.83 | 18.29 | 17.03 | 16.97 | 14.09 | 17.21 | 15.59 | |
| KNM-ER 1470 | 10.51 | 14.20 | 10.30 | 13.56 | 13.17 | 10.88 | 13.30 | 17.24 | 13.40 | 13.12 | 14.20 |

This similarity in the patterning indicated by the distance matrices is reflected in the similarity between the UPGMA phenograms (Sneath and Sokal, 1973) calculated from each (figs 4.1, 4.2). Both phenograms have a cophenetic correlation with the original distance matrices of greater than 0.91 ($P<0.001$). They are similar to each other in that *Pan* and Sts 5 cluster together and then with *A. boisei*; *Homo erectus* clusters with the Neanderthals; the a.m. fossils cluster with negroes and then with Skhul V; and Steinheim clusters with the Neanderthals, *Homo erectus*, a.m. fossils, negroes and Skhul V. They differ in the clustering of OH 24 (with *Homo* – 34 vars, with apes and australopithecines – 25 vars.), KNM–ER 1470 (with apes and australopithecines –. 34 vars, with *Homo* – 25 vars.) and Kabwe (with fossil a.m. *Homo*, negroes and Skhul V – 34 vars, with Neanderthals and *Homo erectus* –25 vars.).

FIGURE 4.1 – UPGMA phenogram from 34 angles and dimensions, cophenetic correlation = 0.93

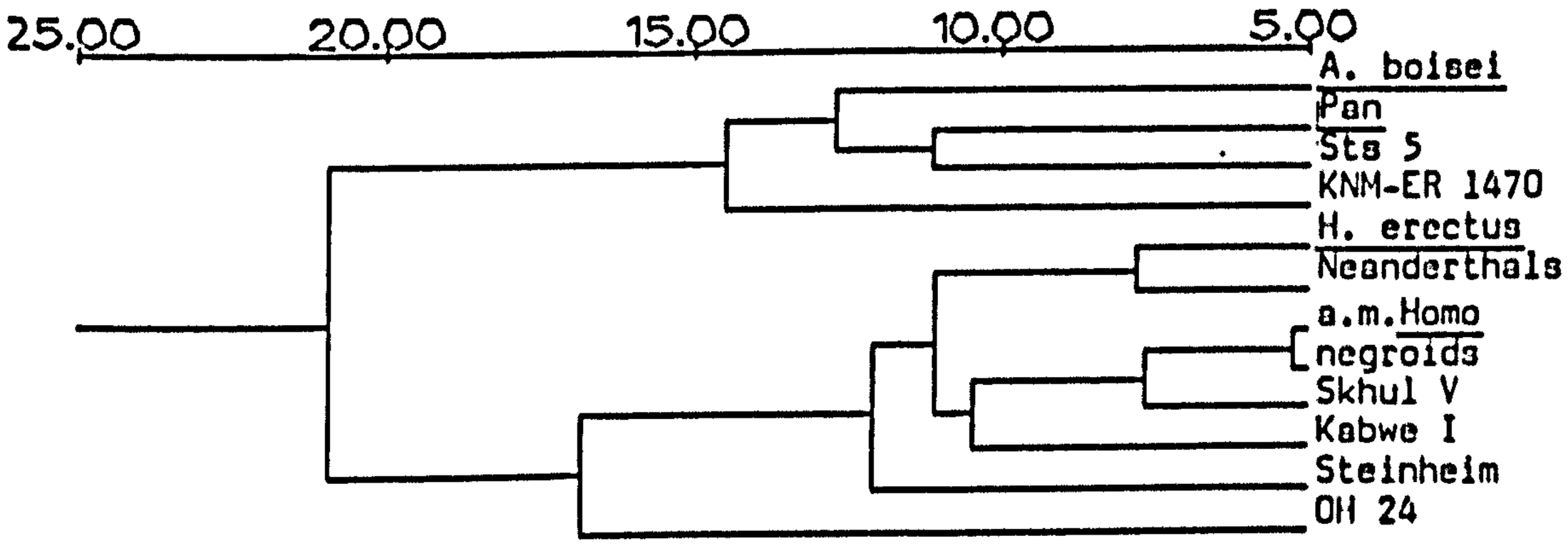



Fig 4.1

FIGURE 4.2 – UPGMA phenogram from 25 scaled projected midline variables, cophenetic correlation = 0.91

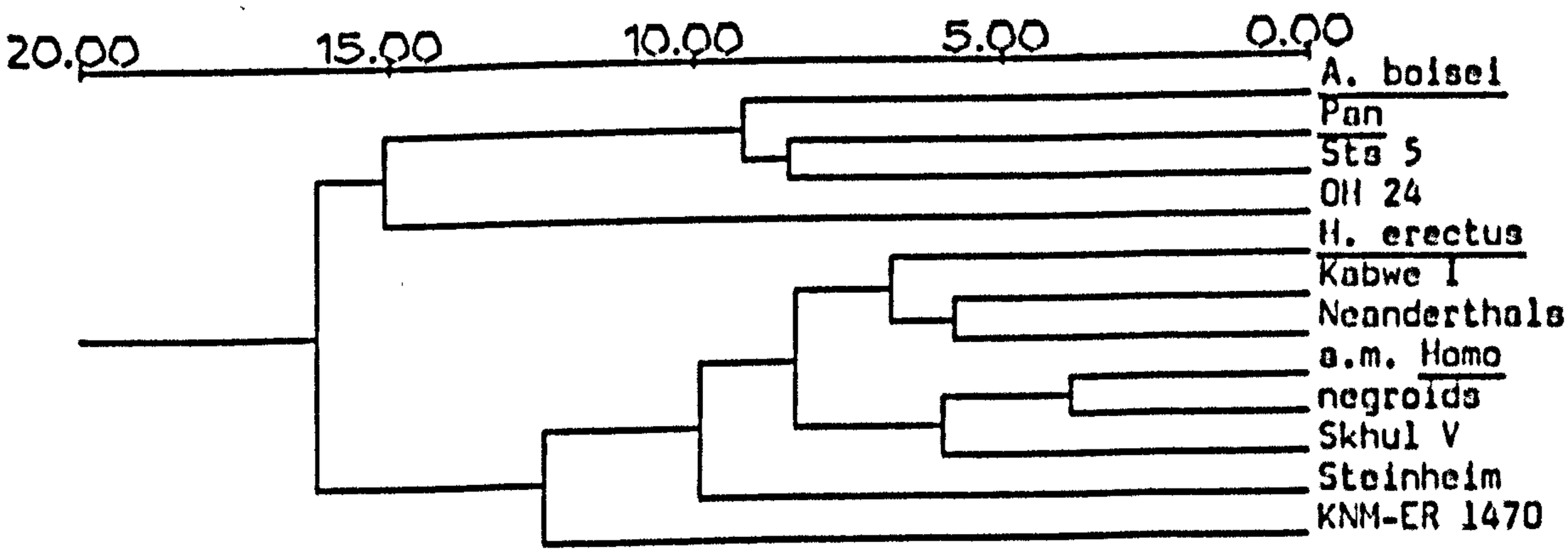


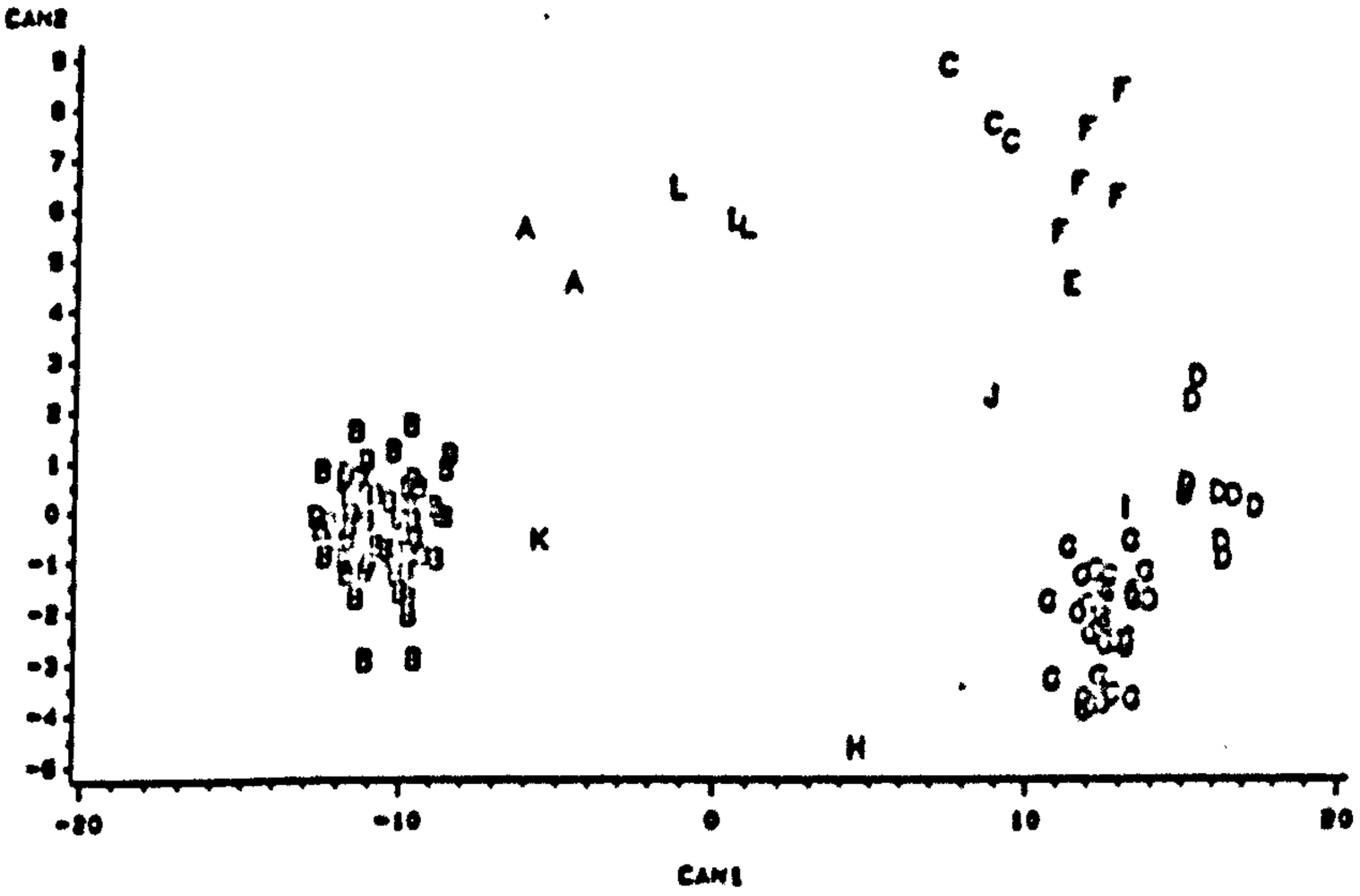

Fig. 4.2

A further indication of the degree of congruence between the distance matrices (tables 4.4 and 4.5) is given by comparing the plots of the scores of groups on the first three canonical axes from each analysis (figs. 4.3 and 4.4). In both analyses the first three axes account for >95% of the total between group variance and the correlation of the scores of OTUs on CAI with their square root of midline area is >0.95 ($P<0.001$). The ordering of groups on canonical axis I in both analyses is *Pan*, Sts 5, *A. boisei*, KNM–ER 1470, OH 24, *H. erectus*, Steinheim, the Neanderthals, Kabwe 1, negroes, Skhul V and fossil a.m. *H. sapiens*, the latter groups being virtually superimposed. This similarity in the ordering of OTUs on the first axis reflects the high correlation of OTU scores on this axis with the size variable. This high correlation is observed despite the data being scaled relative to the size variable. It probably reflects the fact that the principal vector of difference between the OTUs relates to neurocranial expansion and decreasing facial prognathism which in turn heavily influence the magnitude of the size variable (the square root of the midline area).

Along canonical axis II the groups are again ordered in a similar sequence though their scores are mirror–imaged. To one extreme are placed KNM–ER 1470, *H. erectus*, the Neanderthals and Kabwe 1, in an intermediate position are placed *A. boisei*, Steinheim, fossil a.m. *H. sapiens* and Skhul V and towards the other extreme are placed *Pan*, Sts 5, negroes and OH 24. The similarity between the canonical analyses becomes less marked on axis III. In the analysis of 34 variables *A. boisei* occupies one extreme whilst this position is taken by KNM–ER 1470 in the analysis of 25 variables. In the analysis of 34 variables Sts 5 is

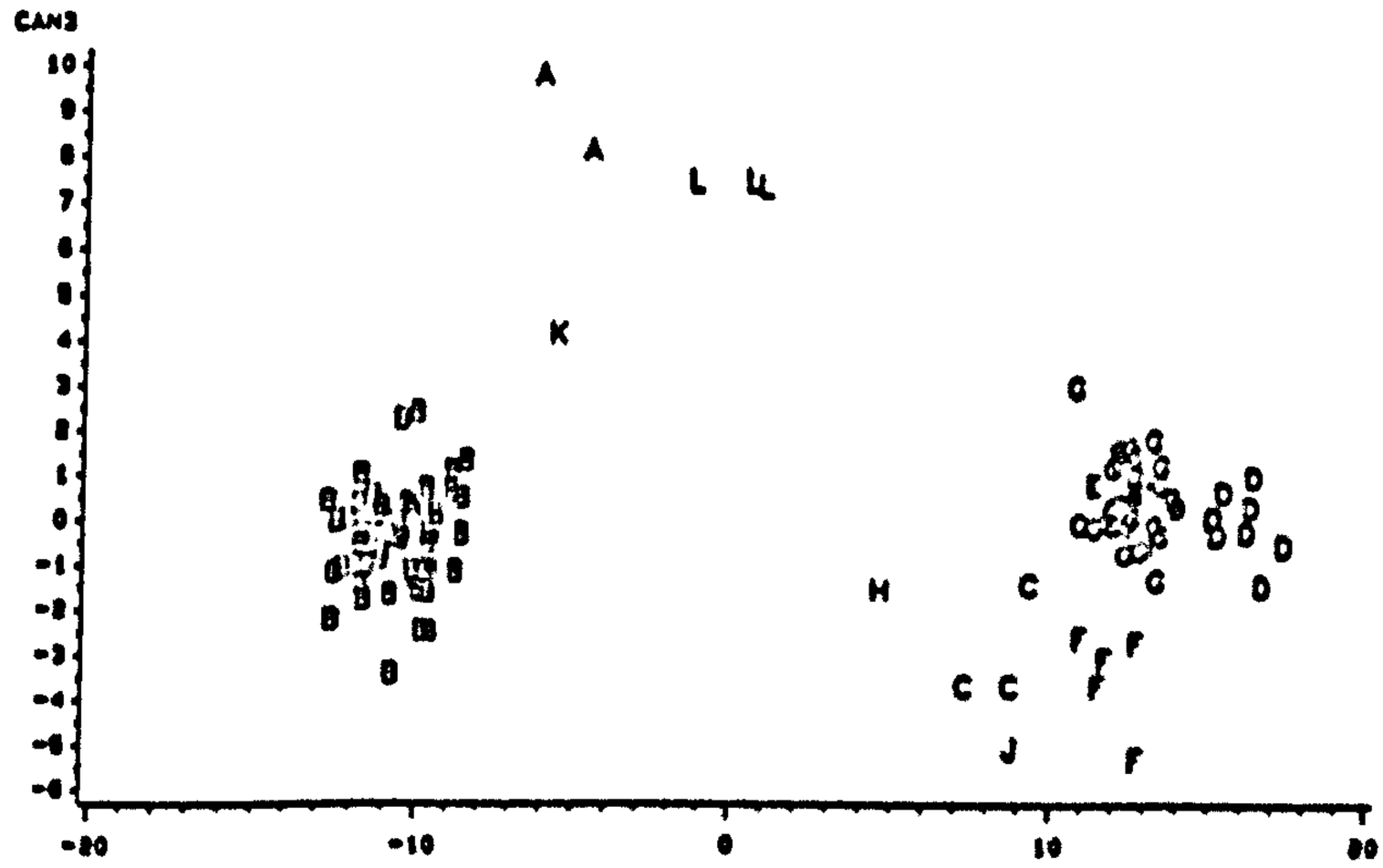
FIGURE 43 – Canonical analysis of 34 logged, scaled linear angular dimensions CAI vs CAII in a) and CAI vs CAIII in b) CAs I + II + III account for > 95% of the between group variance

a)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

b)

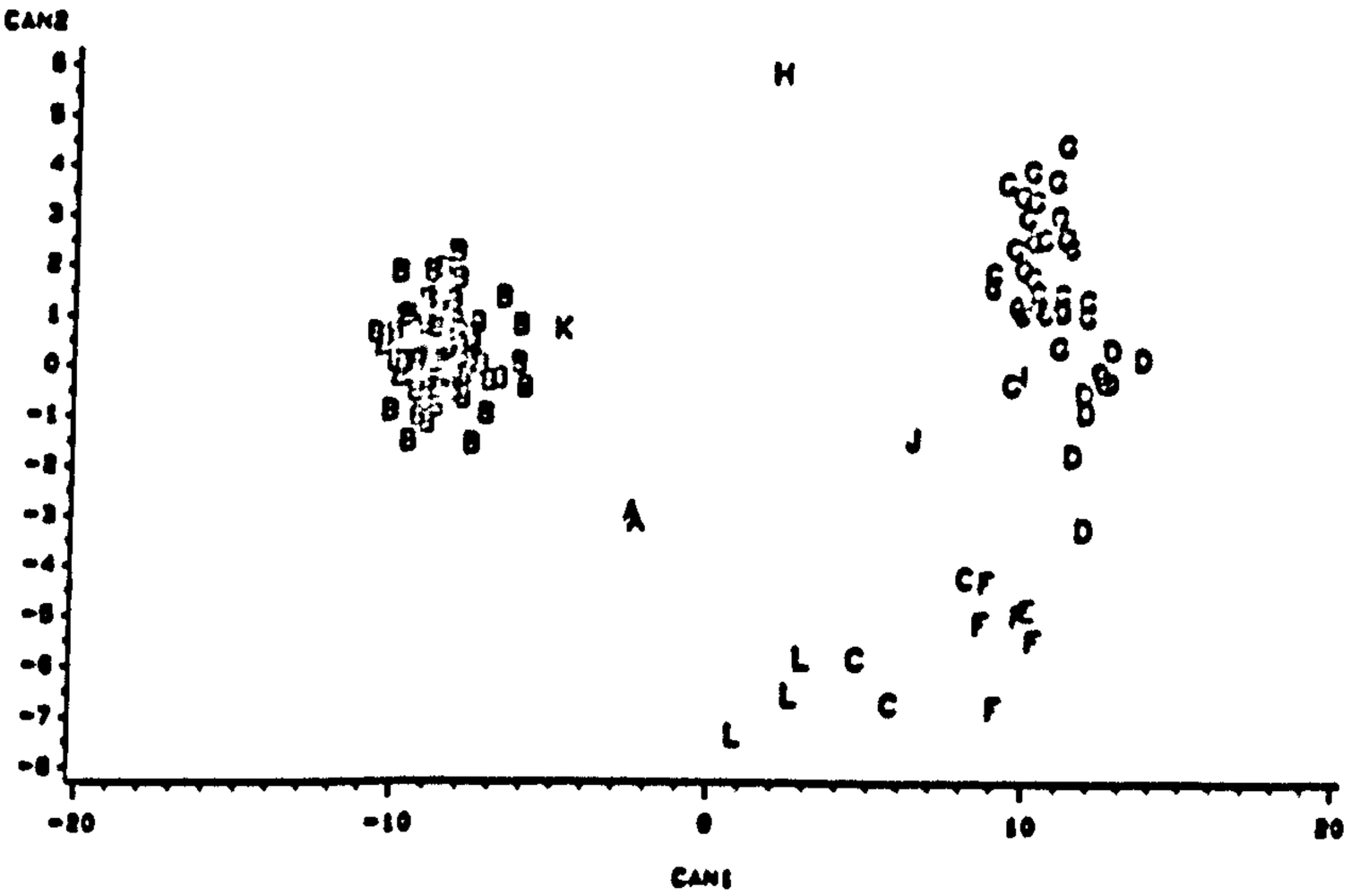



GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

Fig 43

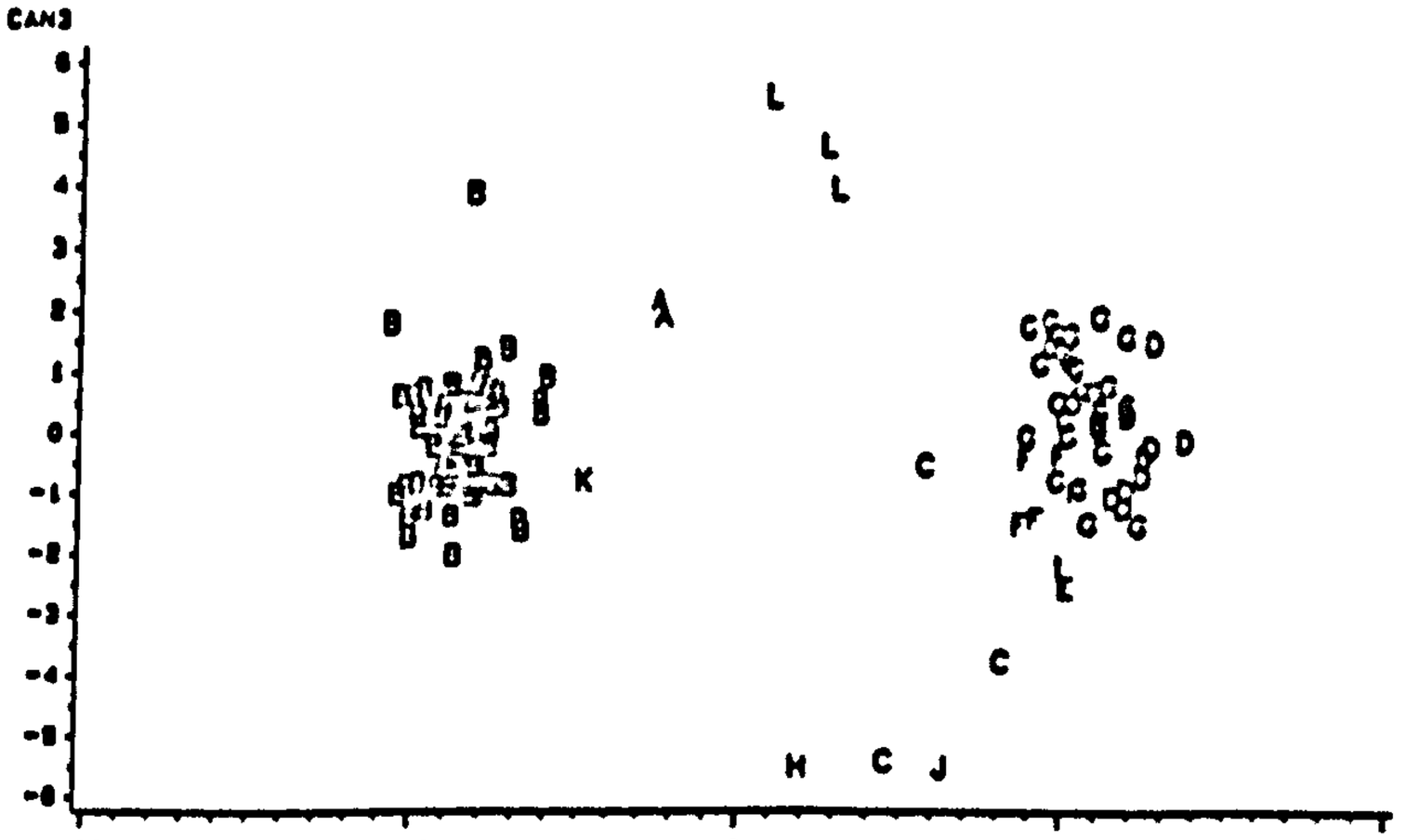
**FIGURE 4.4 – Canonical analysis of 25 logged, scaled midline variables. CAI vs CAII in a) and CAI vs CA III in b). CAs I + II + III account for > 95% of the between group variance**

a)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

b)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

Fig 4.4

more clearly differentiated from *Pan* and Kabwe 1 from the Neanderthals on axis III than is the case in the analysis of 25 variables. Other differences include the more central position of OH 24, and the lesser within group variability in *H. erectus* in the study of 34 variables.

These studies concur with those of chapter 2 in that they indicate a high degree of concordance between the patterns of phenetic relationships indicated by midline and midline plus off–midline data. The differences in result are most clearly appreciated from a comparison of the phenograms and are less obvious from the matrix correlation. The significance of these differences is discussed later.

II. Comparison of the results obtained from Fourier data with those from 25 midline and projected midline variables.

a) the first 20 sine-cosine Fourier coefficients

The matrix of Mahalanobis' distances calculated from the first 20 sine-cosine Fourier coefficients (40 variables in all) is presented in table 4.6. The correlation between this matrix and that from 25 variables (table 4.5) is 0.63 ($P<0.001$). This is considerably less than that between the matrices from 25 and 34 variables ($r=0.94$). The implication is that the pattern of phenetic relationships derived from the Fourier data is different in some respects from that derived from the 25 linear and angular measurements. The difference in result appears to be greater than that encountered in the studies of modern groups (chapter 2).

TABLE 4.6

Mahalanobis' distance matrix calculated from the first 20 scaled sine/cosine Fourier coefficients

| | boi | Pan | erec | a.m. | Kabw | Nean | Negr | OH24 | SkhV | Stei | Sts5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A.boisei | | | | | | | | | | | |
| Pan | 12.93 | | | | | | | | | | |
| H.erectus | 14.13 | 14.51 | | | | | | | | | |
| a.m. H.sapiens | 18.16 | 18.80 | 14.60 | | | | | | | | |
| Kabwe | 19.50 | 21.90 | 18.64 | 15.35 | | | | | | | |
| Neanderthals | 17.99 | 17.68 | 12.52 | 9.19 | 15.35 | | | | | | |
| Negroes | 18.93 | 19.25 | 16.42 | 4.39 | 15.42 | 10.73 | | | | | |
| OH 24 | 19.23 | 21.08 | 20.94 | 16.76 | 23.02 | 18.00 | 16.81 | | | | |
| Skhul V | 22.59 | 21.61 | 19.01 | 11.85 | 14.17 | 14.05 | 11.80 | 22.13 | | | |
| Steinheim | 19.90 | 23.82 | 20.11 | 19.15 | 17.81 | 15.44 | 19.94 | 22.82 | 20.28 | | |
| Sts 5 | 18.85 | 17.73 | 17.40 | 20.48 | 26.94 | 21.39 | 21.89 | 21.85 | 24.76 | 27.12 | |
| KNM-ER 1470 | 15.33 | 13.53 | 13.72 | 11.27 | 17.73 | 14.38 | 11.85 | 18.44 | 16.22 | 22.01 | 19.18 |

In keeping with the findings of chapter 2 the distances calculated from Fourier data are generally larger than those derived from 25 midline variables

though some, between *Pan* and other OTUs and between KNM–ER 1470 and other OTUs, are reduced.

In the studies of chapter 2 this general inflation of distances was largely the result of the greater number of variables used to calculate them (40 as opposed to 25) and it produced only a marginal improvement in overall discrimination (as judged by discriminant analysis). It is not possible to examine the degree of difference in discrimination using discriminant functions when dealing with these fossil groupings because many OTUs are represented by a single cranium and any stepwise method will inevitably omit one or other OTU entirely. It is, however, possible to gain an impression of the relative differences in separation by other methods.

The difference in the pattern of phenetic relationships is emphasised by the table of % differences in relative distances (table 4.7). This was calculated after scaling both distance matrices (tables 4.5 and 4.6) to have the same *Pan* – Negro distance (it was nearly identical between analyses, 19.08 SDU from midline measurements, 19.25 SDU from Fourier data). The difference between each element of the two distance matrices is expressed as a percentage of the distance derived from 25 linear and angular measurements. Negative values indicate a proportionately smaller distance in the matrix from 25 angles and dimensions and positive ones indicate a relatively larger one.

From table 4.7 it can be seen that there are differences in the proportionate distances between groups. The Fourier data have indicated a relatively larger between–OTU difference in the case of all hominid–hominid comparisons with

TABLE 4.7

Matrix of differences in Mahalanobis' distances between the study of 25 scaled midline measurements and 20 scaled sine/cosine Fourier coefficients. Differences are expressed as a percentage of the distances from the study of 25 midline measurements after the two distance matrices have been scaled to have the same *Pan* – Negro distance

| | boi | Pan | ere | a.m. Kabw | Nean | Negr | OH24 | Skhv | Ste | Ste5 |
|---|---|---|---|---|---|---|---|---|---|---|
| A. boisei | | | | | | | | | | |
| Pan | -37.8 | | | | | | | | | |
| H. erectus | -14.9 | 12.8 | | | | | | | | |
| a.m. H.sapiens | -12.1 | 10.5 | -55.8 | | | | | | | |
| Kabwe | -27.9 | -7.7 | -142.8 | -109.9 | | | | | | |
| Neanderthals | -30.9 | 7.6 | -103.4 | -42.5 | -162.3 | | | | | |
| Negroes | -25.5 | 0.0 | -61.6 | -11.6 | -68.3 | -33.8 | | | | |
| OH 24 | -23.4 | -33.1 | -35.5 | -4.7 | -30.6 | -5.3 | -19.2 | | | |
| Skhul V | -49.5 | -11.4 | -106.2 | -100.4 | -69.0 | -78.1 | -92.4 | -56.8 | | |
| Steinheim | -24.9 | -36.7 | -117.1 | -82.5 | -62.5 | -52.4 | -90.8 | -69.0 | -134.0 | |
| Sts 5 | -103.3 | -107.0 | -11.6 | -7.8 | -46.0 | -24.5 | -27.9 | -53.7 | -42.6 | -72.4 |
| KNM-ER 1470 | -44.6 | 5.6 | -32.0 | 17.6 | -33.4 | -31.0 | 11.7 | -6.0 | -20.0 | -66.3 |

the exception of the distances between KNM–ER 1470 and negroes and fossil a.m. *Homo sapiens*. The distances between *Pan* and other OTUs show a more variable pattern of differences (if the matrices had not been scaled the difference in the *Pan*–negro distance would have been 0.9%).

Fourier data have emphasised the distinctiveness of certain fossils. There is a very unequal pattern of differences in distances, in some cases the increase in relative distance has been very large – for instance the distances between Kabwe, fossil a.m. *Homo sapiens*, the Neanderthals and *Homo erectus*, between *Homo erectus*, the Neanderthals, Skhul V and Steinheim, between fossil a.m. *Homo sapiens* and Skhul V, and between Sts 5, *A. boisei* and *Pan* have more than doubled in relative terms.

The differences between the distance matrices are emphasised when the UPGMA phenogram from Fourier data (fig 4.5, cophenetic correlation = 0.82, $P<0.001$) is compared with that from the 25 midline measurements (fig 4.2). Apart from the clustering of *Pan* with *A. boisei* and fossil a.m. *H. sapiens* with negroes the Fourier phenogram contrasts with that from midline measurements in the pattern of associations of virtually every OTU and in that Steinheim, Sts 5 and OH 24 appear as outliers.

A clearer picture of the differences in results can be gained from an examination of the plots of canonical axes. The first five canonical axes from the analysis of Fourier data are plotted in figures 4.6 and 4.7. These five axes account for >95% of the total between-group variance. The percentage of total between-group variance accounted for by the axes contrasts with the situation found in the studies of linear and angular measurements in that relatively more axes are needed to adequately describe between-group relationships.

The scores of OTUs on the first axis have (like those from the study of midline variables) a high correlation ($r=0.95$, $P<0.001$) with the size variable. In keeping with this, the pattern of group dispositions on the first canonical axis derived from Fourier data is similar to that on the first axis calculated from the midline measurements (fig. 4.6 vs 4.4). One extreme is occupied by *Pan* and the other by Skhul V, fossil a.m. humans and negroes. Near to *Pan* are placed Sts 5 and *A. boisei*, next are KNM-ER 1470, *H. erectus* and OH 24, next are Steinheim, Kabwe and the Neanderthals.

FIGURE 4.5 – UPGMA phenogram from 20 scaled sine/cosine Fourier coefficients, cophenetic correlation = 0.82

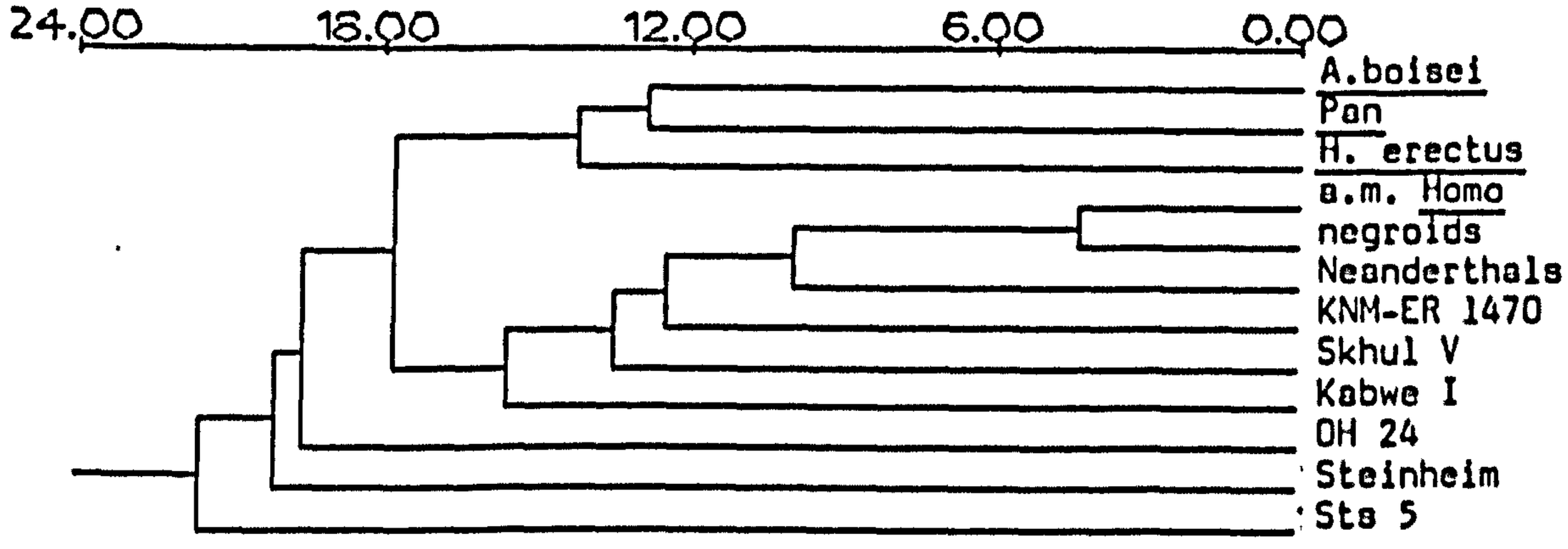
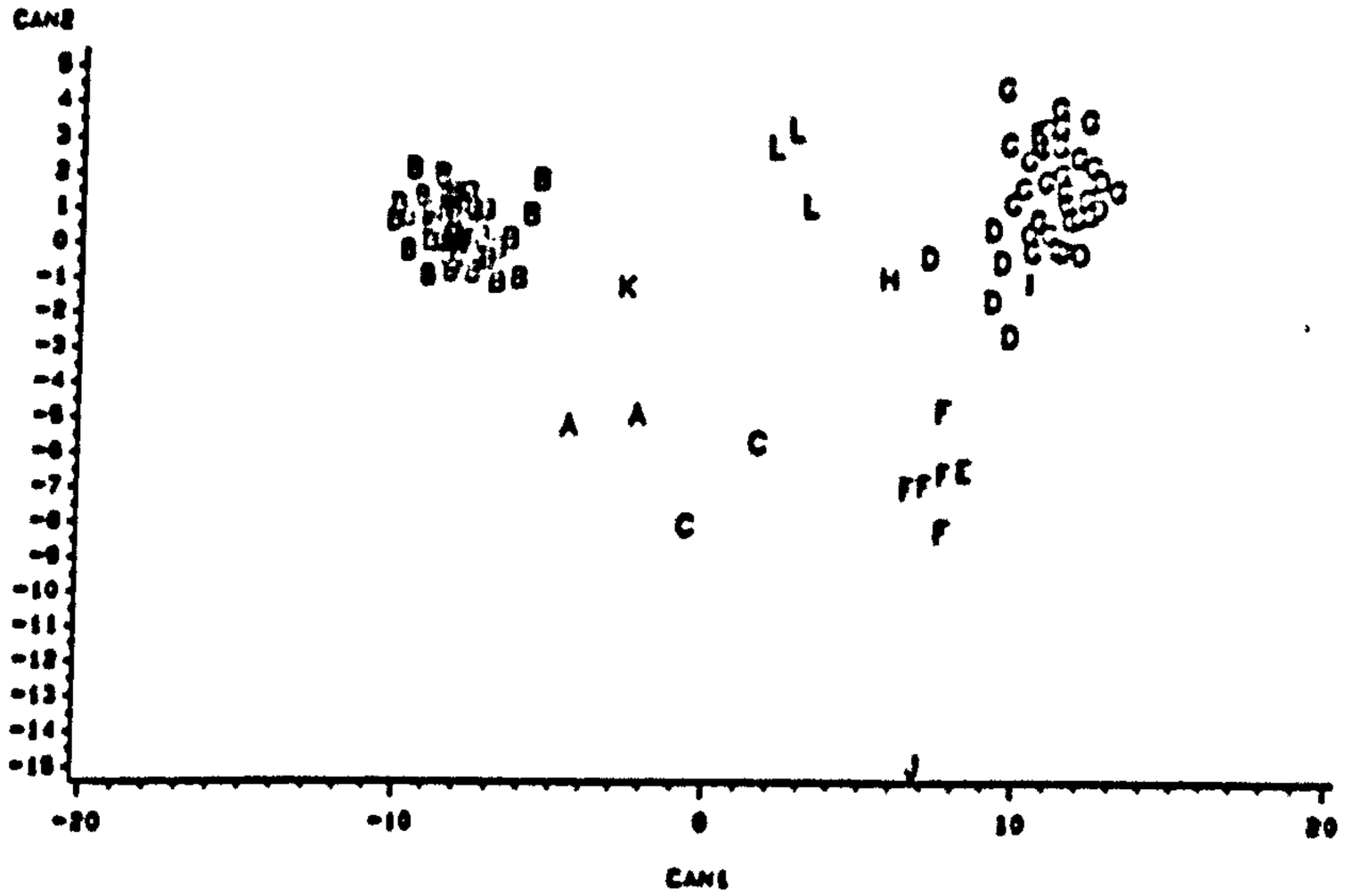



Fig 4.5

FIGURE 4.6 – Canonical analysis of the first 20 scaled sine/cosine Fourier coefficient pairs. CAI vs CA II in a) and CA I vs CA III in b)

a)




b)

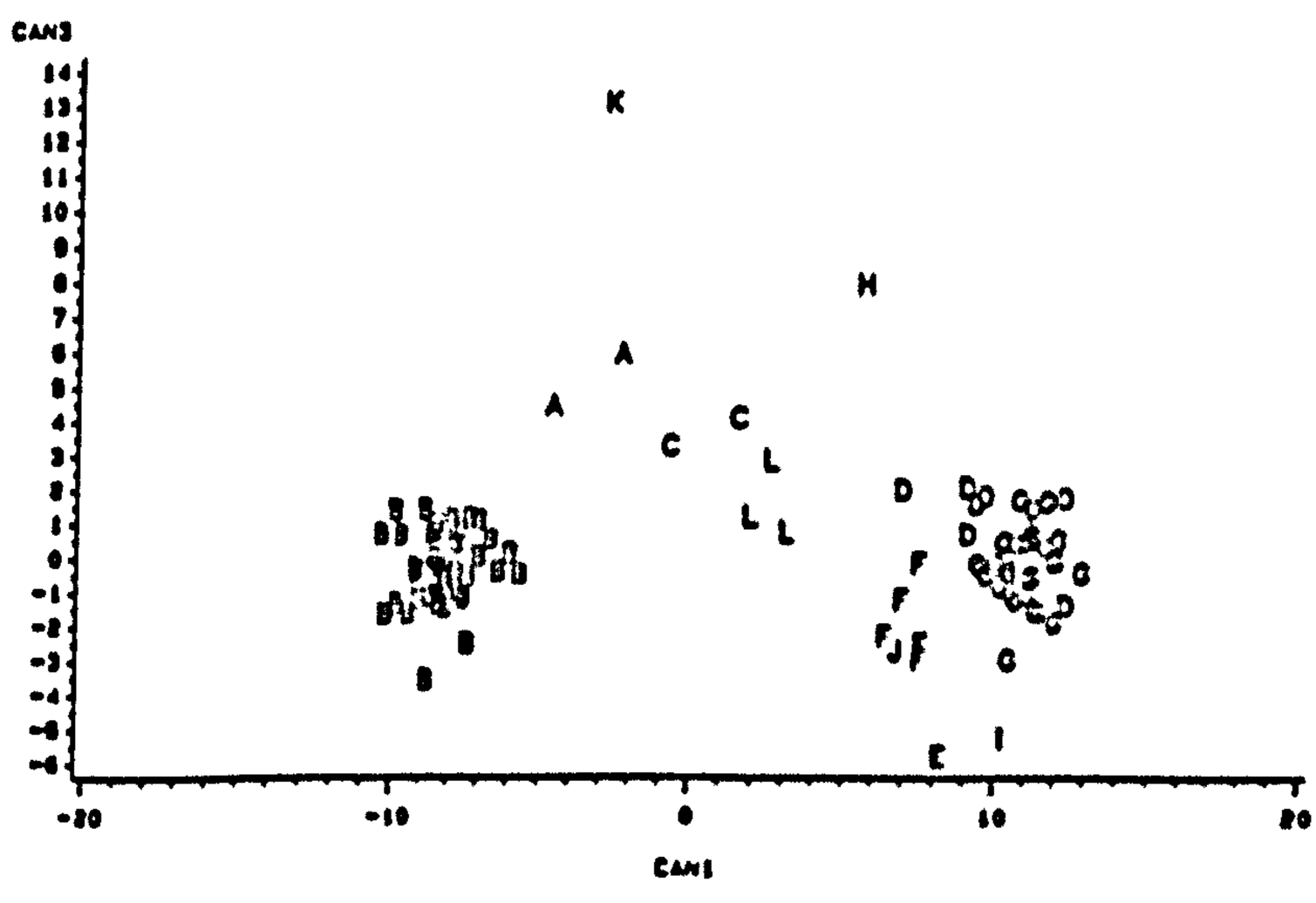
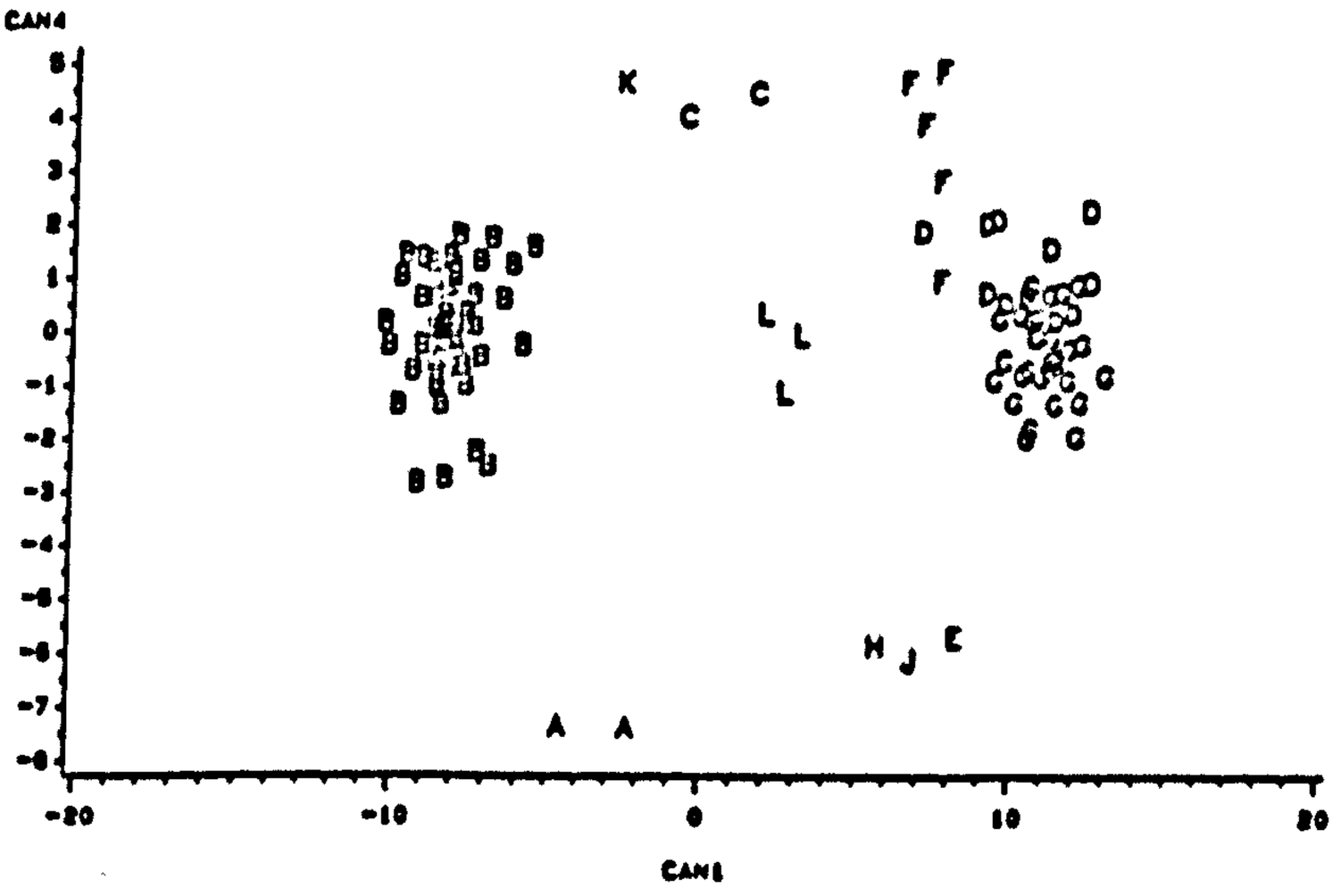



Fig 4.6

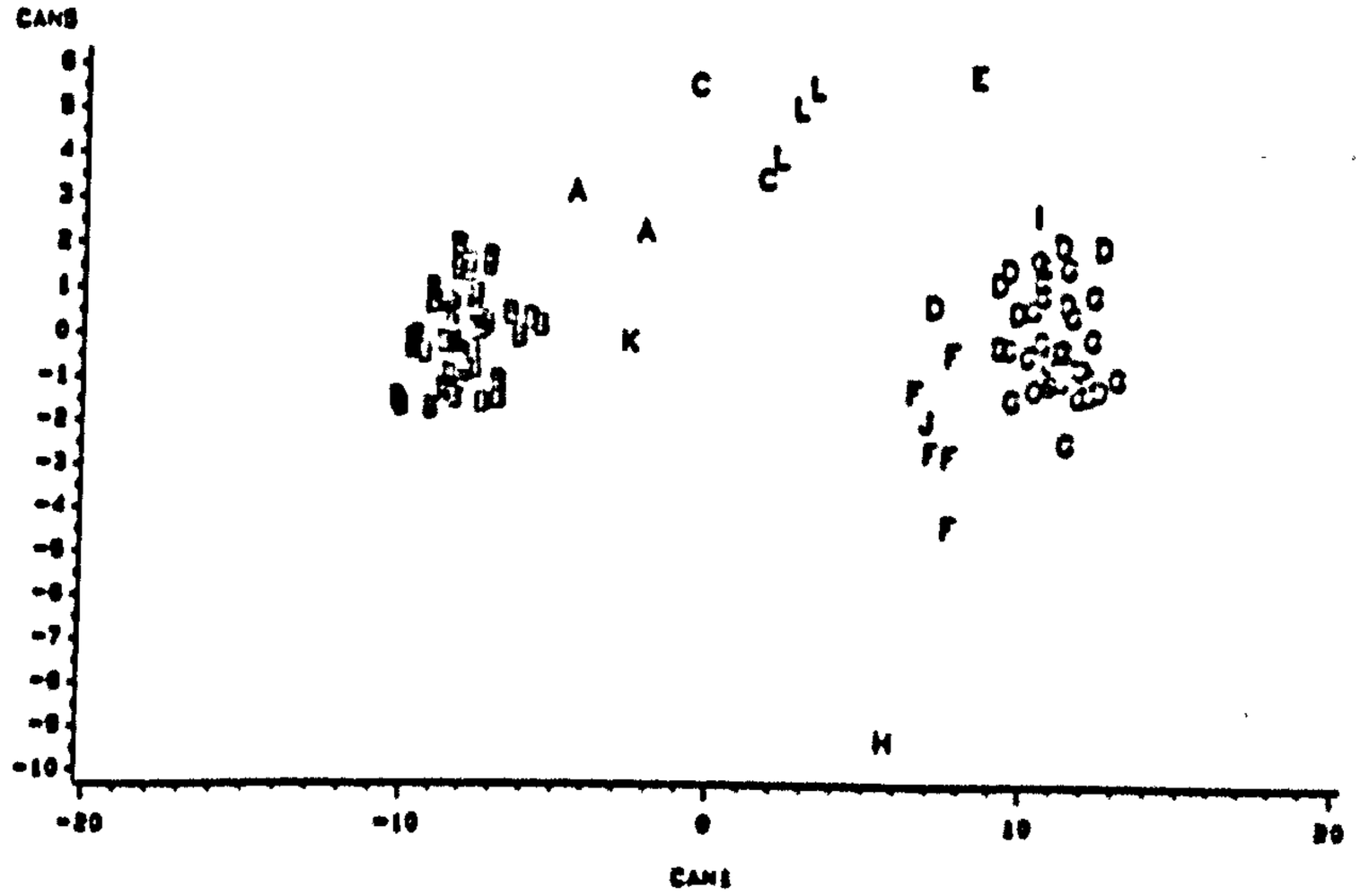
FIGURE 4.7 – Canonical analysis of the first 20 scaled sine/cosine Fourier coefficient pairs. CA I vs CA IV in a) and CA I vs CA V in b). CAs I – V together account for > 95% of the between group variance

a)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

b)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

Fig 4.7

The second canonical axis shows more differences between analyses. In the study of Fourier data and that from 25 midline measurements the fossil a.m. humans, negroes, Skhul V, Sts 5 and *Pan* are placed toward the positive and *H. erectus* and the Neanderthals toward the negative extreme of canonical axis II. In the analysis of Fourier data CAII serves to differentiate Steinheim at its negative extreme whilst it is placed centrally in the analysis of midline variables. Conversely, the analysis of midline data differentiates OH 24 at the positive and KNM–ER 1470 at the negative extreme of CAII whilst they are central in the analysis of Fourier data.

The third canonical axis continues this trend of increasing difference in result between the analyses of Fourier data and of linear and angular measurements. In common to both studies *Pan*, fossil a.m. *Homo*, negroes and Neanderthals occupy similar positions on CA III whilst the other fossils are more widely scattered and occupy locations which differ between analyses.

This pattern of differences between the canonical analyses of Fourier data and midline measurements concurs with that implied by the study of differences in the distance matrices. The differences between fossils on higher axes are generally accentuated by Fourier analysis whilst differences along the *Pan*–negro axis (CAI) are relatively unaltered. The first canonical axis accounts for 80% or more of the total between–group variability in each analysis (34 measurements, 25 measurements and Fourier data) and the distribution of OTUs on this axis is very similar irrespective of which measurement method is used. It has already been noted that the scores of crania on CAI have a high correlation with the

size variable in each study. This probably reflects the significant cranial shape differences which are associated with neurocranial expansion. Fourier data does, however, lead to the impression of greater differences between the fossil OTUs on higher canonical axes.

To summarise, the results of the canonical analysis using the first 20 sine–cosine Fourier coefficients appear to differ from those using linear and angular dimensions. This difference is reflected in the low (though highly significant) correlations between the distance matrices, in the greater relative distances between a number of fossil OTUs and in the differences in phenogram topologies. The study of canonical axes reveals, however, that the underlying pattern of phenetic discrimination as described by CAI is very similar regardless of measurement technique. As higher order axes are compared the degree of similarity between analyses diminishes.

In order to further examine the differences between the results of the studies of Fourier data and of dimensions and angles an analysis was undertaken using the 30 sine–cosine Fourier components which best discriminated between modern groups in the studies of chapter 2.

b) the 30 sine–cosine Fourier components which best discriminated between modern OTUs

The matrix of between fossil Mahalanobis' distances calculated from the 30 Fourier components which best discriminated between the modern groups (chapter

2) is presented in table 4.8. It has a correlation of 0.69 ($P<0.001$) with the matrix calculated from 25 midline measurements. This is marginally higher than that between the matrix from 25 midline measurements and 20 sine–cosine Fourier coefficients ($r=0.63$) and implies a slightly greater degree of congruence in the pattern of phenetic relationships.

## TABLE 4.8

Mahalanobis' distance Matrix calculated from 30 scaled Fourier components

| | boi2 | Pan | erec | a.m. | Kabw | Mean | Negr | Oll24 | SkhV | Ste1 | Ste5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A. boisei | | | | | | | | | | | |
| Pan | 11.90 | | | | | | | | | | |
| H. erectus | 13.23 | 13.01 | | | | | | | | | |
| a.m. H.sapiens | 15.76 | 17.07 | 12.18 | | | | | | | | |
| Kabwe | 16.11 | 19.23 | 15.74 | 12.13 | | | | | | | |
| Neanderthals | 15.04 | 15.22 | 10.08 | 7.02 | 13.55 | | | | | | |
| Negroes | 16.11 | 17.21 | 13.73 | 4.09 | 12.84 | 9.27 | | | | | |
| Oll 24 | 12.90 | 15.40 | 15.28 | 14.11 | 18.18 | 13.42 | 14.31 | | | | \ |
| Skhul V | 18.71 | 19.45 | 16.15 | 10.16 | 12.39 | 12.19 | 11.89 | 19.35 | | | |
| Steinheim | 12.75 | 16.26 | 11.90 | 11.80 | 13.89 | 11.07 | 12.82 | 12.85 | 14.87 | | |
| Ste 5 | 14.80 | 12.44 | 13.06 | 17.69 | 21.46 | 16.53 | 18.23 | 16.97 | 20.36 | 17.85 | |
| KNM-ER 1470 | 13.21 | 12.25 | 10.67 | 9.29 | 13.40 | 10.52 | 9.76 | 14.35 | 12.84 | 11.37 | 13.37 |

The distance matrix from 30 Fourier components was further compared with that from 25 midline measurements by calculating a table (table 4.9) of % differences in distances relative to the *Pan* – negroid distance. There are widespread differences in inter–OTU distances but these are, on average, reduced relative to those demonstrated in table 4.7.

Table 4.9 shows a greater than two fold increase in the relative distances between Kabwe and *Homo erectus* and the Neanderthals and between Skhul V and the negroes. This is similar to the relative increase in the between OTU

distances when 20 sine–cosine Fourier coefficients were studied (table 4.7).

TABLE 4.9

Matrix of differences in Mahalanobis' distances between the study of 25 scaled midline measurements and 30 scaled sine/cosine Fourier components. Differences are expressed as a percentage of the distances from the study of 25 midline measurements after the two distance matrices have been scaled to have the same *Pan* – negro distance

| | boi | Pan | erec | a.m. | Kabw | Nean | Negr | OH24 | SkhV | Stel | Sts5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A. boisei | | | | | | | | | | | |
| Pan | -41.9 | | | | | | | | | | |
| H. erectus | -20.3 | 12.5 | | | | | | | | | |
| a.m. H. sapiens | -8.9 | 9.1 | -45.4 | | | | | | | | |
| Kabwe | -18.2 | -5.8 | -129.3 | -85.5 | | | | | | | |
| Neanderthals | -22.4 | 11.0 | -83.2 | -21.8 | -139.0 | | | | | | |
| Negroes | -19.5 | 0.0 | -53.0 | -16.3 | -56.8 | -29.3 | | | | | |
| OH 24 | 7.4 | -8.7 | -10.6 | 1.4 | -15.4 | 12.2 | -13.5 | | | | |
| Skhul V | -38.5 | -12.1 | -95.9 | -92.2 | -65.3 | -72.8 | -116.8 | -53.3 | | | |
| Steinheim | 10.5 | -4.4 | -67.9 | -25.8 | -41.8 | -22.2 | -37.2 | -6.5 | -91.9 | | |
| Sts 5 | -78.5 | -62.4 | 6.3 | -4.2 | -31.3 | -7.6 | -19.1 | -33.3 | -31.2 | -26.9 | |
| KNM-ER 1470 | -39.3 | 4.4 | -14.8 | 24.0 | -12.8 | -7.2 | 18.6 | 7.7 | -6.2 | 2.2 | -20.0 |

The correlation of the distance matrix from 30 Fourier components with that from 20 Fourier coefficients is 0.86 ($P<0.001$). This is comparable with that between the matrices from 25 midline and 34 midline plus off–midline measurements ($r=0.94$). Comparison of the distance matrix (table 4.6) from 20 Fourier coefficients (40 variables) with that from 30 Fourier components (table 4.8) suggests a reduction in the average distance between OTUs in the latter. This is in keeping with the reduced number of variables.

The distance matrix from 30 Fourier components is further compared with that from 20 coefficient pairs in table 4.10 by calculating % differences between the latter and the former after scaling the matrices to have the same *Pan*–negro distance. In table 4.10 positive values indicate a smaller relative inter–OTU

difference in the matrix from 30 components. This reduction is not evenly spread, and is greater for some fossils, e.g. Steinheim OH 24 and Sts 5 than for others, e.g. Kabwe, Skhul V.

TABLE 4.10

Matrix of differences in Mahalanobis' distances between the study of 20 scaled sine/cosine Fourier coefficients and 30 scaled sine/cosine Fourier components. Differences are expressed as a percentage of the distances from the study of 20 sine/cosine Fourier coefficients after the two distance matrices have been scaled to have the same *Pan* – negro distance

| | bois | Pan | erec | a.m. | Kabw | Nean | Negr | OH24 | SkhV | Stei | Sts5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A. boisei | | | | | | | | | | | |
| Pan | -2.9 | | | | | | | | | | |
| H. erectus | -4.7 | -0.3 | | | | | | | | | |
| a.m. H. sapiens | 2.9 | -1.6 | 6.7 | | | | | | | | |
| Kabwe | 7.6 | 1.8 | 5.5 | 11.6 | 1.3 | | | | | | |
| Neanderthals | 6.5 | 3.7 | 9.9 | 14.6 | 1.3 | | | | | | |
| Negroes | 4.8 | 0.0 | 6.5 | -4.2 | 6.9 | 3.4 | | | | | |
| OH 24 | 25.0 | 18.3 | 18.4 | 5.8 | 11.7 | 16.6 | 4.8 | | | | |
| Skhul V | 7.4 | -0.7 | 5.0 | 4.1 | 2.2 | 3.0 | -12.7 | 2.2 | | | |
| Steinheim | 28.3 | 23.6 | 22.7 | 31.1 | 12.8 | 19.8 | 28.1 | 37.0 | 18.0 | | |
| Sts 5 | 12.2 | 21.5 | 16.0 | 3.4 | 10.1 | 13.6 | 6.8 | 13.1 | 8.0 | 26.4 | |
| KNM-ER 1470 | 3.6 | -1.3 | 13.0 | 7.8 | 15.5 | 18.2 | 7.9 | 13.0 | 11.5 | 41.2 | 10.4 |

These results indicate that the 30 sine–cosine Fourier components suggest a greater degree of distinctiveness in the morphology of certain fossils than do the 25 midline measurements. Furthermore, in the case of the Kabwe cranium and the Skhul V cranium the degree of distinctiveness is similar to that implied by the 20 sine–cosine Fourier coefficients. In some cases, e.g. Sts 5, OH 24 and Steinheim it is less.

The UPGMA phenogram derived from the distance matrix calculated from 30 sine–cosine Fourier components is presented in fig. 4.8. The distances implied by this phenogram correlate 0.78 ($P<0.001$) with those in the distance

FIGURE 4.8 – UPGMA phenogram from 30 sine/cosine Fourier components, cophenetic correlation = 0.78

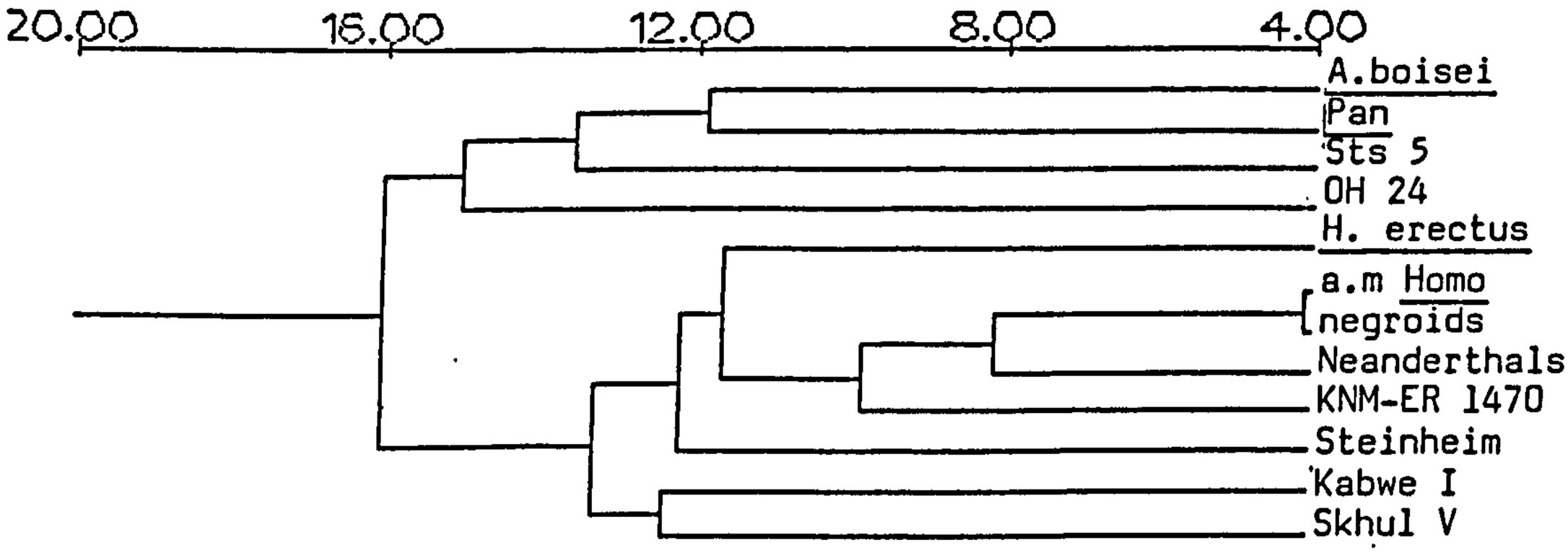


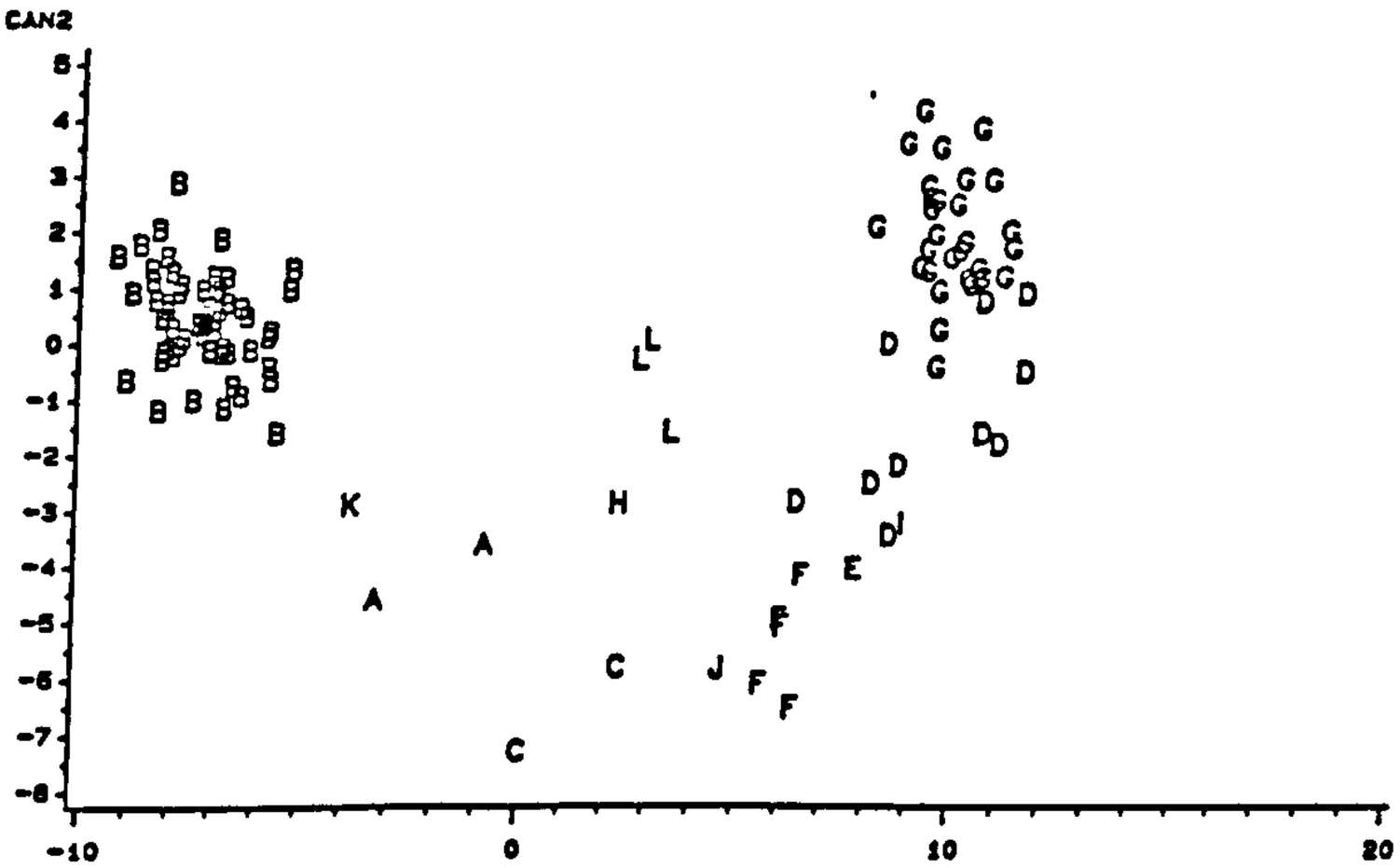

Fig 4.8

matrix. This compares with a cophenetic correlation of 0.82 for the phenogram from the distance matrix derived from 20 sine–cosine Fourier coefficients. The topology of the phenogram from 30 Fourier components is more like that from 25 midline variables, than is the phenogram calculated from 20 sine–cosine Fourier coefficients, and shows a similar pattern of clustering of *A. boisei*, *Pan*, Sts 5 and OH 24. It does, however, differ from Figure 4.2 in the order of clustering of the other OTUs in that Skhul V and Kabwe are more distinctive, the Neanderthals appear more like fossil a.m. *Homo* and KNM–ER 1470 appears more like modern hominids.

The plots of OTU scores on canonical axes I–V are presented in figures

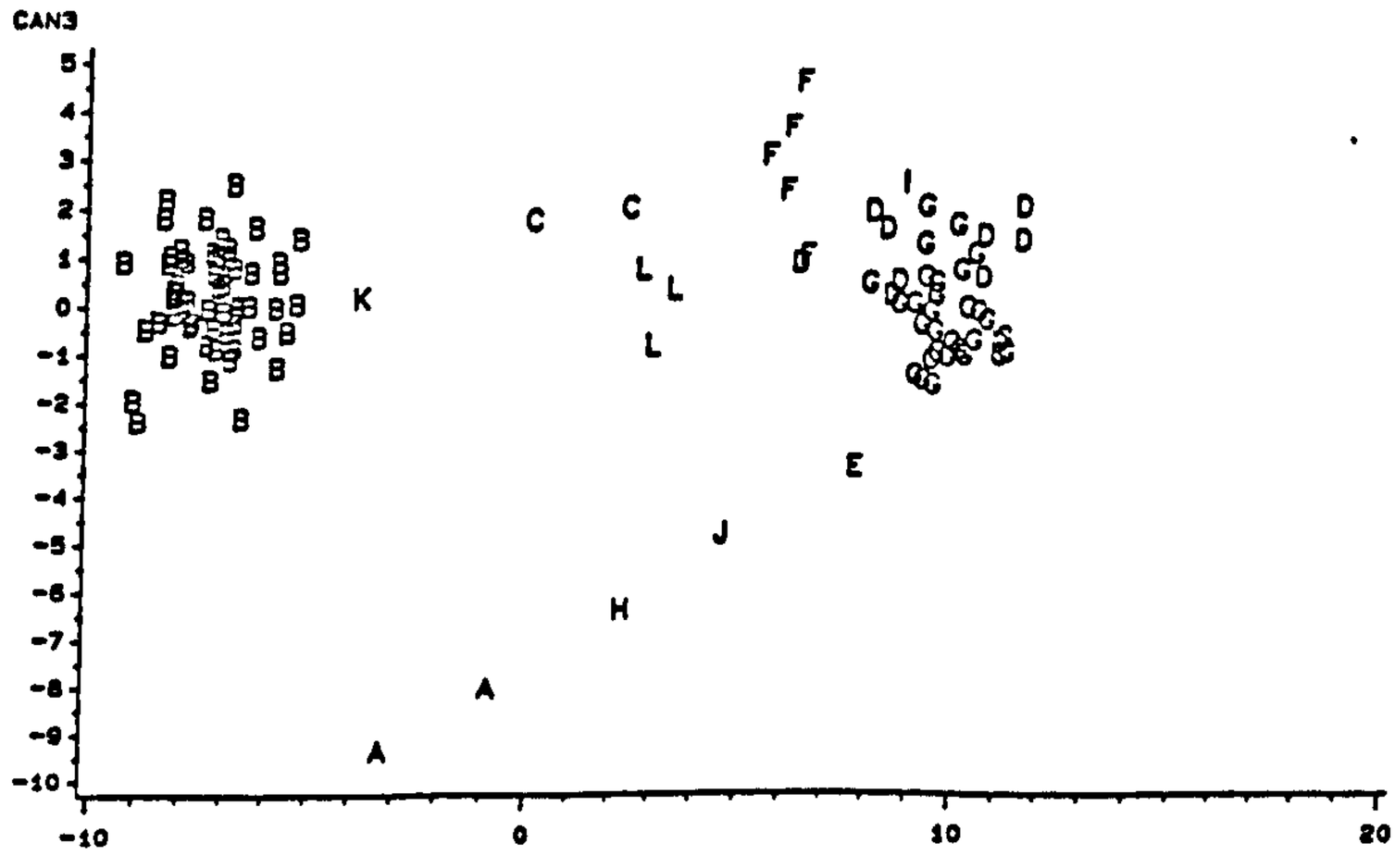
FIGURE 4.9 – Canonical analysis of scaled 30 sine/cosine Fourier components CAI vs CA II in a) and CA I vs CA III in b)

a)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

b)

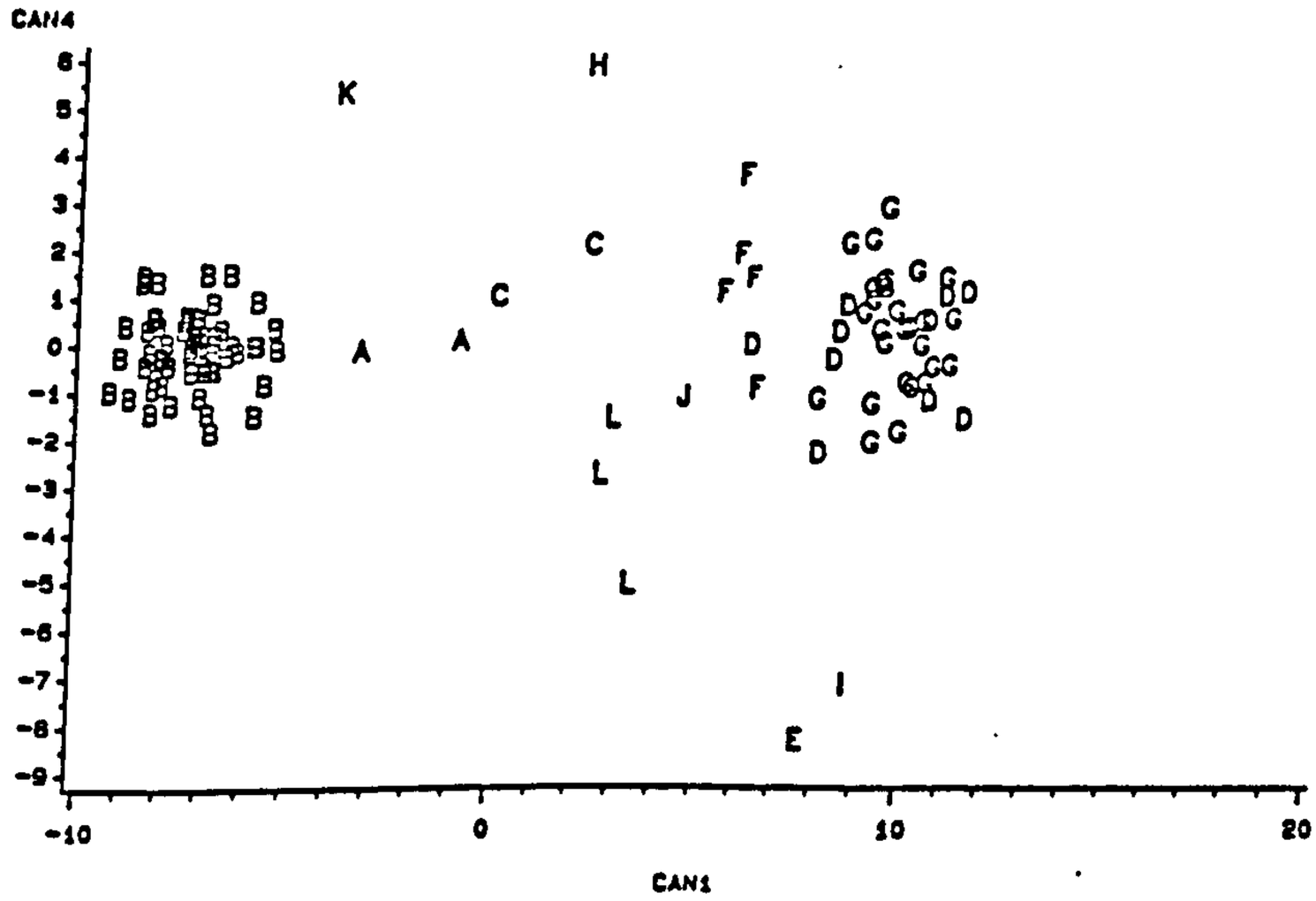



GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

Fig 4.9

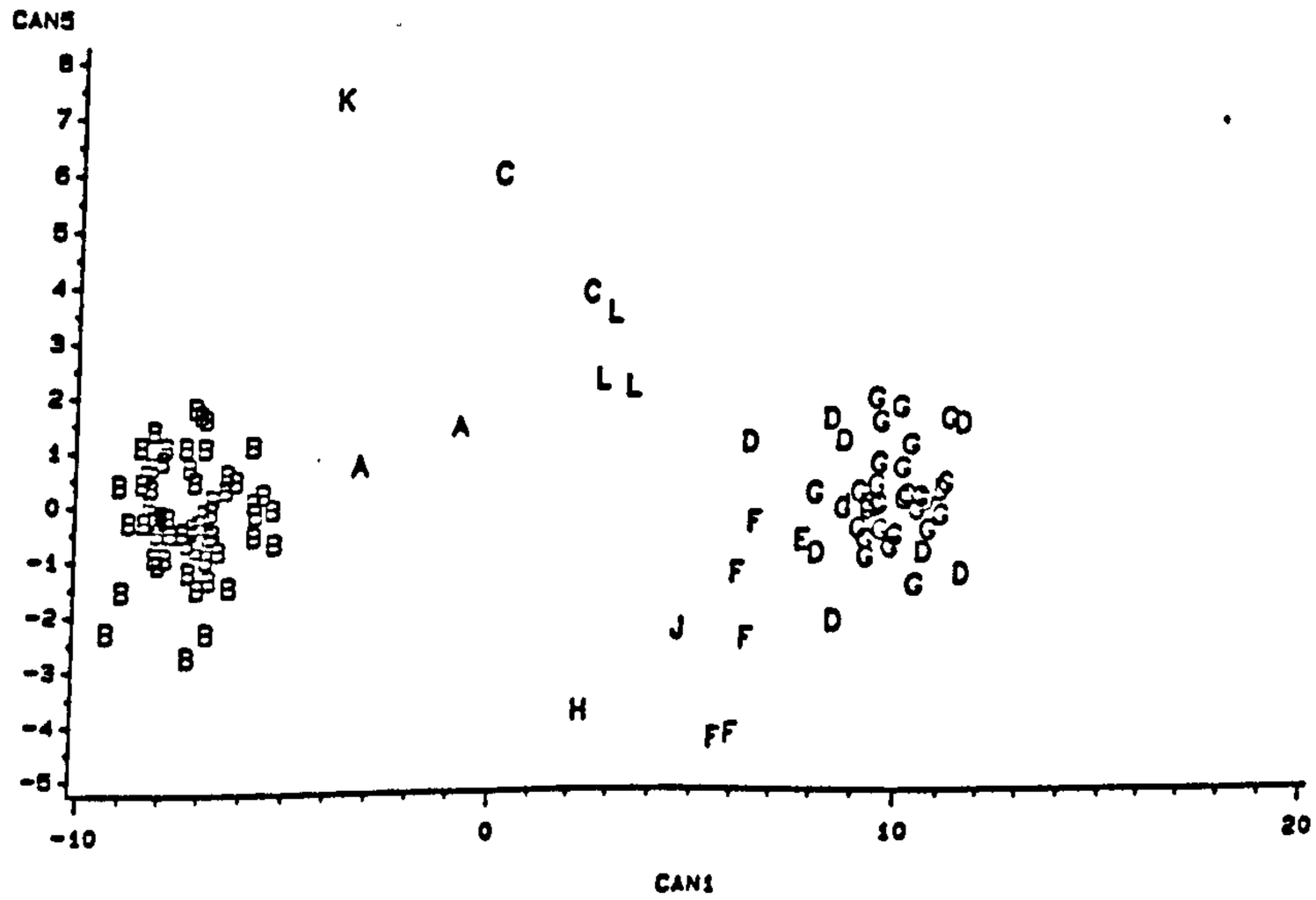
FIGURE 4.10 – Canonical analysis of scaled 30 sine/cosine Fourier components CA I vs CA IV in a) and CA I vs CA V in b). CAs I – V together account for > 95% of the between group variance

a)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

b)




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

Fig 4.10

4.9 and 4.10. The first five axes are needed to account for >95% of the between OTU variance. On canonical axis I the OTUs are arranged in nearly the same order as on CAI from the analysis of 25 midline variables (fig. 4.4).

On CAII *Pan*, the negroes, fossil a.m. *Homo*, Kabwe, the Neanderthals, *Homo erectus*, *A. boisei* and Sts 5 are arranged in a comparable order to that shown in figure 4.4. The reconstructions of KNM–ER 1470 and OH 24 are placed more centrally and the Steinheim cranium is placed more towards the negative pole.

On CAIII the modern groups, fossil a.m. *H. sapiens*, Steinheim, Kabwe, OH 24 and Sts 5 are located in similar positions to those they occupy in the analysis of 25 midline variables. Of the other crania the Neanderthals occupy a more positive position, *Homo erectus* and KNM–ER 1470 are placed more centrally and *A. boisei* is shifted to the extreme negative pole.

The higher canonical axes serve to distinguish certain fossil groups. On CAIV (fig. 4.10) Sts 5 and OH 24 occupy the positive pole whilst Kabwe and Skhul V occupy the negative. On CAV the positive pole is occupied by Sts V, nearer the centre are placed *H. erectus* and KNM–ER 1470.

In general the scores of OTUs on canonical axes in this analysis show a better correspondence with the analysis of 25 measurements than did the canonical analysis of 20 Fourier coefficients. This is confirmed by the correlations of OTU scores on CAs I–IV, listed in table 4.11. Invariably the scores on canonical axes from the study of 30 components show a higher correlation with those from the study of 25 measurements than do those from the study of 20

coefficient pairs. Only the correlations on CAI are significant ($P<0.05$) but the differences in absolute terms allow an assessment of similarity (see Sneath and Sokal, 1973).

**TABLE 4.11**

**The correlation of scores of OTUs on canonical axes in the studies of Fourier data with the scores of OTUs on canonical axes in the analysis of 25 midline measurements**

| | 20 Coeffs | 30 comps. |
|---|---|---|
| CA I | 0.93 | 0.97 |
| CA II | 0.32 | 0.41 |
| CA III | 0.07 | 0.18 |
| CA IV | 0.21 | −0.21 |

n.b. only correlations on CA I are significant at $P<0.05$

In summary the study of 30 sine−cosine Fourier components, like that of 20 Fourier coefficients, has indicated a degree of distinctiveness in certain fossils which does not agree with the phenetic relationships suggested by linear and angular measurements. The level of agreement between the distance matrix from 30 Fourier components and that from linear and angular measurements is, however, marginally greater than was the case when 20 Fourier coefficients were compounded. The differences in the distance matrices are reduced and the canonical analysis has shown that these differences are concentrated in higher components.

# DISCUSSION OF RESULTS

## I. A Comparison of the results from the analyses of different types of data

The studies described above have indicated:

1. A high degree of concordance between the studies of midline linear and angular measurements and those from midline plus off-midline measurements.
2. A lesser degree of agreement between the study of 30 sine-cosine Fourier components and that of 25 midline measurements.
3. An even smaller degree of concordance between the study of 20 sine-cosine Fourier coefficients and that of 25 midline measurements.

The simplest explanation for this pattern of differences is that each study uses a different set of variables and, as such, describes different aspects of cranial morphology. The degrees of congruence between studies may simply reflect the extent to which they are based on variables which describe similar aspects of morphology.

It was noted in chapter 2 and earlier in this chapter that Fourier data include variables which are "noisy". These variables may not serve to differentiate between groups (except in the sense of adding to the dimensionality of the multivariate analyses, n.b. more traditional measurements may also suffer from this problem) and may describe aspects of shape which are either common to

all OTUs or which are entirely spurious and reflect only measurement error. In chapter 2 it was pointed out that the errors of measurement which result from tracing an outline on a digitising tablet are generally of the form of high frequency undulations (because of tremor and pixel size) and therefore tend to be concentrated in higher order Fourier components.

The studies of chapter 2 provided a detailed examination of ways of eliminating "noise" from Fourier data. Increasing numbers of Fourier components were added successively to discriminant analyses in an attempt to optimise discrimination and minimise variable number. The studies in which successively higher order coefficient pairs were added to discriminant analyses identified the first 20 as being optimal in the description of differences between modern apes and men. These first 20 pairs of sine–cosine Fourier coefficients allow the reconstruction of outlines with a high degree of accuracy. If the ability to reconstruct is unimportant it is possible to further reduce "noise". In this case variables are selected for their usefulness in separating groups (as assessed by variance ratio) and are added successively to discriminant analyses. The outcome of these analyses (chapter 2) indicated that 30 sine–cosine components (see figure 2.17) were optimal in the problem of identifying the provenance of modern hominoid crania.

It is impossible to use such methods to determine the best components for differentiating the fossil OTUs in this study (because some OTUs have only one member) but it would seem reasonable to assume that the 30 components which discriminated well between men and apes may also be effective between

apes, fossil hominids and men. In any case, the data will certainly be less "noisy" than the first 20 sine–cosine Fourier coefficients as far as the modern and fossil a.m. OTUs are concerned.

A further explanation for the degree of incongruence between the analyses of this chapter may therefore be that the Fourier data are giving rise to entirely spurious separations between OTUs because of "noise".

In order to assess whether the contrasts in shape differences indicated by Fourier data and linear and angular measurements are a result of measurement error or of fundamental differences in the way in which the data describe morphology it is necessary to consider the extent of agreement between the phenetic relationships indicated by the studies of this chapter and those implied by the studies of other workers.

II. A comparison of the results of this study with those from the studies of other workers.

The phenetic relationships of each fossil are considered in turn:

*a. A. boisei*

The species *Australopithecus boisei* is represented in this study by one specimen from Olduvai, OH 5, and one from Koobi Fora, KNM–ER 406.

Of the studies described in this chapter:

a) The distance matrix from 34 measurements indicates that *A. boisei* is closest to Sts 5 (11.72 SDU) next are KNM–ER 1470 (13.07 SDU) and *Pan* (13.70 SDU) (table 4.4). The other hominid OTUs are more distant and, of these *Homo erectus* is the closest.

b) The same pattern of relationships holds in the study of 25 midline measurements (table 4.5).

c) The analysis of 20 Fourier coefficients (table 4.6) indicates a different pattern of phenetic relationships, *A. boisei* is closest to *Pan* (12.93 SDU), *Homo erectus* is next (14.13 SDU) followed by KNM–ER 1470 (15.33 SDU). Sts 5 is no closer to *A. boisei* than any other hominid OTU.

d) When the matrix of Mahalanobis' distances from the study of 30 Fourier components is examined, *A. boisei* is again closest to *Pan* (11.90 SDU) but Steinheim, OH 24, KNM–ER 1470 and *Homo erectus* are nearly equidistant from *A. boisei* (about 13 SDU). Again, Sts 5 is no closer to *A. boisei* (14.8 SDU) than are a number of other hominid OTUs.

These studies all agree in indicating that the cranial morphology of *A. boisei* is generally ape–like (see Ashton, 1981). The linear and angular measurements indicate a degree of similarity to Sts 5 and this is in keeping with the common generic attribution of these specimens by some workers (e.g. Tobias, 1967, but see Grine, 1981, and earlier).

In a multivariate study of facial morphology Bilsborough and Wood (1988) have noted that *A. boisei* have faces which are longer and broader with absolutely and relatively deeper malar regions than those of *A. africanus*. Their studies indicate that the facial morphology of KNM–ER 1470 is basically hominine but in some respects mimics that of robust australopithecines. Consistent with the findings of Bilsborough and Wood each of the current studies suggests a degree of similarity between *A. boisei* and KNM–ER 1470 and this is most pronounced when facial breadths are included in the data (34 measurements).

Bilsborough (1973) undertook a multivariate study of the proportions of the cranial vault which indicated considerable differences between *A. boisei* and *A. africanus*, particularly in vault height and frontal morphology. His canonical analysis affords a large degree of distinction to *A. boisei* on the combination of canonical axes I and II though the Mahalanobis' distance matrix from his study shows the most similar cranial vaults to *A. boisei* are those of *H. erectus*. It is noteworthy that the present studies also indicate a degree of similarity between the cranial morphology of *A. boisei* and that of *Homo erectus*. This is particularly pronounced in the studies of Fourier data and is in keeping with the distance matrix based upon vault dimensions published by Bilsborough (1972). That the

similarity is most pronounced in the studies of Fourier components may well reflect the fact that, unlike the linear and angular measurements, these data completely describe vault morphology (note, in the studies of Fourier data KNM–ER 3733, which has the most rounded vault, was omitted). Fourier data do not give disproportionate weighting to the morphology of regions with more identifiable landmarks (e.g. face and base) and which can therefore be measured more thoroughly.

This even description of morphology may well explain the fact that Sts 5 is apparently quite distinct from *A. boisei* in the studies based upon Fourier data (again consider the findings of Bilsborough, 1973).

In a later study Bilsborough (1984) demonstrated that in a combination of analyses based upon a wide range of cranial regions *A. boisei* was highly distinctive. This is, again, in keeping with the results of each of the current studies. Despite the relationships discussed above the Mahalanobis' distances between *A. boisei* and each other OTU are generally large and in the plots of canonical axes from each study (figs.4.3, 4.4, 4.6, 4.7, 4.9, 4.10) the crania are markedly separated from other OTUs on one or other axis.

*b) A. africanus – Sts 5*

The species *A. africanus* is represented in this study by a single cranium from Sterkfontein, Sts 5. The study of 34 linear and angular measurements indicates that Sts 5 is most similar to *Pan* (11.10 SDU) and *A. boisei* (11.72 SDU) and that it is widely separated from all other OTUs (table 4.4). This

result is similar to that from the study of 25 midline measurements (table 4.5). It is reflected in the clustering of Sts 5 with *Pan* and *A. boisei* in the phenograms from both studies (figs. 4.1, 4.2) and in the closeness of Sts 5 to these OTUs in the canonical analyses of these sets of data (figs 4.3, 4.4).

By contrast, the studies of Fourier data indicate more distinctiveness in the cranial morphology of Sts 5. This is particularly pronounced in the analyses of 20 paired sine–cosine Fourier coefficients where Sts 5 is very widely separated from all OTUs (nearest overall to Asiatic *H. erectus*, 17.40 SDU and see canonical axis 3, fig. 4.6 and clusters last with all other OTUs in the UPGMA Phenogram fig. 4.5). In the absence of Fourier data from other representatives of *A. africanus* it is impossible to be certain of the reliability of this result. When the data which were "noisy" in the studies of modern groups are removed, however, the pattern of relationships of Sts 5 changes considerably.

The study of 30 sine–cosine Fourier components suggests a degree of distinctiveness in the cranial morphology of Sts 5 but indicates that it is most similar overall to *Pan* (12.44 SDU). The results, again, indicate a likeness to Asiatic *H. erectus* (13.06 SDU), and to *A. boisei* (14.80 SDU). This pattern of relationships is more like that derived from angles and measurements and this is reflected in the UPGMA phenogram from the 30 Fourier components (fig. 4.8) in which Sts 5 clusters with *A. boisei* and *Pan*. The canonical analysis of this data further confirms these phenetic relationships with Sts 5 being close to *Pan* on CAs I, II and III, and widely separated on CAs IV and V.

All of the analyses agree in that they point to a general similarity of Sts 5 to Pan though the studies of Fourier data consistently emphasise some distinctiveness. A degree of similarity to *A. boisei* is also demonstrated especially by the studies of angles and dimensions (though Sts 5 and *A. boisei* are close on CAs I and II in the studies of Fourier data). All analyses indicate, however, that Sts 5 has an overall cranial morphology which is more like *Pan* than *A. boisei*. Few other phenetic studies of hominids include ape data. One of the few which does is that of Boyce (1969) who, by contrast with the present study found a consistently greater similarity between *A. africanus* and *A. crassidens* (from Swartkrans) than between *A. africanus* and *Pan*. This difference in result may well reflect the greater facial and masticatory development which is found in East african "robust" australopithecines (Grine, 1981, Bilsborough and Wood, 1988).

The general similarity of the midline projection of Sts 5 to that of Asiatic *H. erectus* indicated from the studies of Fourier data again disagrees with the findings of Boyce (1969) and of other workers (e.g. Bilsborough, 1984) who used more anatomically extensive data. This result should, however, be interpreted in the light of the facts that the distances between Sts 5 and *Homo erectus* are generally very large, the Fourier data are scaled, and that, in common with *Homo erectus*, Sts 5 has a neurocranium which is relatively large with respect to the viscerocranium, and possesses in the midline, a glabellar torus with supraglabellar sulcus, a frontal rising above the upper margin of the orbit and an occipital with lower scale less curved than the upper (see Howells, 1980 and the casts). It seems, again, that neurocranial similarity has proportionally more

weighting in studies of Fourier data than in those of linear and angular measurements.

### c) Early *Homo*, OH 24 and KNM–ER 1470

All of the studies of this chapter agree in indicating a relatively large difference in cranial morphology between KNM–ER 1470 and OH 24. In both of the distance matrices from the studies of angles and dimensions the furthest OTU from KNM–ER 1470 is OH 24 (tables 4.4 and 4.5). Those from Fourier data (tables 4.6 and 4.8) point to a greater relative similarity. This finding is consistent with the suggestion from the earlier studies that viscerocranial morphology predominates in the phenetic similarity implied by angles and dimensions whilst neurocranial similarity predominates in the analyses of Fourier data.

The Mahalanobis' distance between male and female gorillas which was calculated in chapter 2 from 25 angles and dimensions was 5.5 SDU and from 20 sine cosine Fourier coefficients, 6.4 SDU. This compares with a distance of more than 16 SDU between KNM–ER 1470 and OH 24 from the equivalent studies in this chapter. These findings indicate that it is highly unlikely that the fossils represent sexual morphs of the same species, a conclusion which concurs with those of Chamberlain (1987) and Chamberlain and Wood (1987) but disagrees with that of Stringer (1986). Other workers, e.g. Lieberman *et al.* (1988) have shown that there is considerable variation in early *Homo*. They compared the degree of difference between KNM–ER 1470 and KNM–ER 1813 with the

degree of sexual dimorphism in *Gorilla* and concluded that it is unlikely that the differences between these two crania can be explained on the basis of sexual dimorphism.

The studies of angles and dimensions both indicate that KNM–ER 1470 shows a degree of similarity to *A. boisei* (tables 4.4 and 4.5). Considering that these data seem to give emphasis to viscerocranial similarity (see above), this is consistent with the findings of Bilsborough and Wood (1988) and with the suggestion made by some workers (Walker, 1976, Krantz, 1977) that KNM–ER 1470 should be included in *Australopithecus*. The results of the studies of Fourier data, however, suggest a greater difference in cranial proportions between KNM–ER 1470 and *A. boisei*. The distance matrices (tables 4.6, 4.8) indicate a much greater similarity to fossil a.m. *Homo* than to any other OTUs including *A. boisei*. Again this finding is consistent with the different emphasis of the Fourier data and with the more bulbous neurocranium of KNM–ER 1470. It does not lend support to the inclusion of KNM–ER 1470 in *Australopithecus*.

The phenetic affinities of OH 24, as judged by both the studies of Fourier data and those of linear and angular measurements, are less clear. All analyses indicate that it is widely removed from other OTUs (tables 4.4, 4.5, 4.6 and 4.8). In the plots of canonical axes (figs. 4.3, 4.4, 4.6, 4.9 and 4.10) it is distant from other OTUs on the combination of at least two axes from each study. This is consistent with the outcome of a cladistic analysis by Chamberlain and Wood (1987) in which Olduvai *H. habilis* appears to be "a relatively primitive hominid that nonetheless shares some derived characters with other post–*A. afarensis*

hominid taxa". The fact that the large distance between OH 24 and other OTUs is emphasised by both the Fourier data and angles and dimensions might indicate that OH 24 is distinctive in both neurocranial and viscerocranial proportions.

d) *Homo erectus*

The analyses using Fourier data differed from those using linear and angular dimensions in not including KNM–ER 3733. Since early African *Homo erectus* has a different cranial morphology from that of the Asiatic representatives (e.g. Stringer, 1984, Wood, 1984, Bilsborough and Wood, 1986) no direct comparison between studies is possible.

Despite this difference all of the studies agree in indicating that Neanderthals are most similar to *Homo erectus*. In the study of 25 angles and dimensions the distance between *Homo erectus* and Neanderthals is 6.1 SDU and between *Homo erectus* and the Kabwe cranium 7.6 SDU (table 4.5). When 9 off–midline dimensions (mainly breadths) are also taken into account (study of 34 angles and dimensions) the distance from *Homo erectus* to the Neanderthals is 7.78 SDU and to the Kabwe cranium, 11.03 SDU. This disproportionate increase in the *Homo erectus* – Kabwe distance indicates that Kabwe differs more from *Homo erectus* in relative cranial and facial breadths (data scaled for midline area) than do the Neanderthals.

In contrast to the studies of angles and dimensions, those using Fourier data indicate a much greater relative distance between *Homo erectus* and the Kabwe cranium. The Neanderthals are closest to *Homo erectus* in both studies (12.52

SDU – 20 coeffs., 10.08 SDU – 30 comps.); next closest is KNM–ER 1470 (13.72 SDU – 20 coeffs., 10.67 SDU – 30 comps.); next closest are fossil a.m. *Homo sapiens*, Negroes and then other OTUs (see tables 4.6 and 4.8). The Kabwe cranium is more widely separated being 18.64 SDU away from *Homo erectus* in the study of 20 Fourier coefficients and 15.74 SDU in that of 30 components.

A multivariate study of cranial proportions by van Vark (1984) indicated that Asiatic *Homo erectus* is closer (Mahalanobis' $D^2$) to recent crania than are Steinheim and Broken Hill (Kabwe); in turn, Steinheim and Kabwe appeared close to each other. In general this result is not borne out by the distance matrices from the studies presented here. Kabwe and Steinheim are not mutually close (see below) and Kabwe is generally closer to fossil a.m. *Homo* than is *Homo erectus*. The Steinheim cranium is further from fossil a.m. *Homo* than is *Homo erectus* in all of the studies except that of 30 Fourier components.

The differences between the studies of Fourier data and those of angles and dimensions may be the result of the different composition of the groups of *H. erectus* in each. The studies of Fourier data include only Asiatic *Homo erectus* which is considered to exhibit a number of autapomorphies (Stringer, 1984, Wood, 1984, and Wood in Bilsborough and Wood, 1986). These autapomorphies might be expected to render the *H. erectus* group relatively less like other OTUs, and this is, indeed what is found (see the comparisons of distance matrices, tables 4.7 and 4.9).

It is clear from the preceding discussions, however, that the studies of Fourier data differ from those of angles and dimensions because of the different ways in which the data describe cranial morphology. The greater difference between *Homo erectus* and the Kabwe cranium and the relative proximity of KNM–ER 1470 and fossil a.m. hominids to *H. erectus* (though distances are large) in the studies of Fourier data may reflect aspects of cranial morphology to which the Fourier data are more sensitive than are the angles and dimensions.

On the one hand the linear and angular measurements indicate a moderate degree of similarity between *Homo erectus*, the Kabwe cranium and the Neanderthals. On the other, the Fourier data, whilst indicating some similarity between the Neanderthals and *Homo erectus*, point to a greater degree of distinctiveness in *Homo erectus*. The above consideration of the results with respect to the phenetic affinities of other OTUs has suggested that the principal difference between analyses of Fourier data and those of linear and angular dimensions relates to the lesser relative weighting given to viscerocranial and basicranial morphology by the Fourier data. This is, in turn, a consequence of the greater ease with which landmarks can be identified on the viscerocranium and cranial base.

It may be, therefore, that the greater distinctiveness in *Homo erectus* in the analyses of Fourier data occurs because the sample in these studies comprises two low vaulted Asiatic representatives of which the cast of "*Pithecanthropus IV*" is heavily reconstructed and the cast of "*Sinanthropus*" is almost entirely sculpted. The apparent similarity with the Kabwe cranium when linear and angular

measurements are studied probably reflects similarity in the facial and basicranial regions more than in the vault.

e) Archaic *Homo sapiens*, Kabwe and Steinheim

In the analyses of linear and angular dimensions the Kabwe and Steinheim crania show a degree of similarity to Neanderthals and more modern *Homo* (tables 4.4 and 4.5). The Steinheim cranium appears more distinctive than the cranium from Kabwe and this is reflected in the UPGMA phenograms and the canonical analyses (figs. 4.1, 4.2, 4.3 and 4.4).

In the studies of Fourier data, however, the Kabwe cranium is at least as distinctive as Steinheim (tables 4.6 and 4.7, figures 4.5–4.10). The Kabwe cranium is more widely separated from the Neanderthals (see CAs III and IV in figures 4.9 and 4.10, and CAs IV and V in figure 4.7) than is the case in the studies of linear and angular measurements (see figures 4.3 and 4.4 and appendix B). In all of the studies the two crania show little affinity for each other and both appear to share some similarities with modern forms, though in different ways (as reflected by the different patterns of associations on canonical axes).

The degree of difference which is demonstrated between the Steinheim and Kabwe crania is consistent with the phylogenetic model of hominid evolution proposed by Brauer (1984). In this model the Kabwe cranium represents a population of archaic *Homo sapiens* which is phylogenetically distinct from the line which later gave rise to Neanderthals and which includes Steinheim. It should be noted, however, that in the analyses of angles and dimensions and of

20 Fourier coefficients Kabwe is more like Neanderthals than is the Steinheim cranium. The finding of a consistent and relatively large distance between Steinheim and Kabwe contradicts the results of the multivariate studies of cranial morphology undertaken by van Vark (1984). His finding was that these crania are relatively close (in terms of Mahalanobis' distances).

The results of Stringer's (1974a) analysis of variables from the whole cranium of a number of fossil hominids (his analysis number 14) indicated that Steinheim, Kabwe and the Neanderthals form a triangle of phenetic relationships (again, not agreeing with findings of van Vark, 1984) and that these OTUs are nearly equidistant from each other. Furthermore, his analysis places a group of Upper Paleolithic crania considerably further away from Steinheim and Kabwe than are the Neanderthals. Of the studies presented here all agree in that Steinheim is more nearly equidistant from fossil a.m. *Homo*, Neanderthals and Kabwe whilst the studies of angles and dimensions disagree with those of Fourier data in placing the Kabwe cranium relatively closer to fossil a.m. *Homo* and Neanderthals.

The disagreements between these analyses and those of other workers, between the results obtained by different workers and between the analyses of angles and dimensions and those of Fourier data are most likely a result of the different aspects of shape described by the different variables used in the studies.

f) The Neanderthals

In the studies of 34 angles and dimensions the most similar OTU to the Neanderthals appears to be *Homo erectus* (7.78 SDU, table 4.4). This contrasts with the study of 25 midline and projected midline measurements where the Neanderthals are closer to the Kabwe cranium (5.8 SDU) than to *Homo erectus* (6.10 SDU). The difference in result is most likely a consequence of the lack of data relating to cranial breadths in the 25 variable analysis and indicates a relatively wider face and base in the Kabwe cranium.

By contrast, in both studies of Fourier data the Neanderthals are nearest to fossil a.m. *Homo sapiens*. The group comprising *Homo erectus* is more distant and the Kabwe cranium is even further removed (tables 4.6 and 4.8). The Steinheim cranium is more widely removed from the Neanderthals than is Kabwe in all of the studies except that of 30 Fourier components (compare tables 4.4, 4.5, 4.6 and 4.8).

The matrix of Mahalanobis' distances calculated by Stringer (1974a) in his analysis (number 14 in his study) of a suite of cranial measurements from a number of fossil hominids indicates that the Kabwe cranium is nearer to Neanderthals (44 $SDU^2$) than is the Steinheim cranium (61 $SDU^2$). His study did not include representatives of *Homo erectus*. He further noted, from a series of multivariate studies, that "the distance between 'classic' Neanderthal and anatomically modern populations ...is always relatively large ...thus the results cast doubt on the possibility of a close relationship between the 'classic' Neanderthals and the Upper Paleolithic populations".

The results of the analyses in the current study do not agree entirely with the findings of Stringer. Steinheim is closer to the Neanderthals than is Kabwe in the study of 30 Fourier components and in both studies of Fourier data fossil a.m. populations are closer to the Neanderthals than any other OTUs.

The results of the current studies show greater agreement with those of van Vark (1984). His multivariate analysis of cranial dimensions indicates that the Neanderthals are closer to Asiatic *Homo erectus* than any other OTU ($D^2$ = 15.6). Of the crania common to his and to the current analyses, next nearest to Neanderthals are his Upper Paleolithic group, then recent men, then Kabwe and finally Steinheim ($D^2$ = 32.5, 39.1, 39.6, 43.5 respectively).

g) Skhul V

In all of the studies of linear and angular measurements and Fourier data the modern negroes and a.m. fossils are nearly equidistant from and are the nearest OTUs to Skhul V, next are the Neanderthals and the Kabwe cranium which are, again, nearly equidistant (tables 4.4, 4.6, 4.5 and 4.8).

Stringer's analysis of cranial measurements from diverse anatomical regions (analysis 14) places Hottentots and Tasmanian aborigines nearest to Skhul V, next is his sample of Upper Paleolithic crania, other modern and fossil a.m. populations are approximately as far away and of the crania common to his study and the current ones the Kabwe cranium is closer to Skhul V than are the Neanderthals. These results generally concur with those of the current analyses as do those of Howells (1970) in which Skhul V appears most like modern

populations and less like "classic" Neanderthals.

h) Anatomically modern fossils of *Homo sapiens*

The relationships of the a.m. fossils have already largely been considered in the earlier discussions. However, it is a consistent finding of all of the studies described in this chapter that the a.m. fossils are very similar to the modern negro population. This is reflected in the distance matrices (tables 4.4, 4.5. 4.6, and 4.8), UPGMA phenograms and canonical analyses (figs 4.1 to 4.10). This high degree of similarity is consistent with the findings of all other workers (see the review presented earlier).

## CONCLUDING DISCUSSION

The studies presented in this chapter have set out to further examine the applicability and utility of Fourier analysis relative to linear and angular measurements in describing hominoid cranial morphology.

In the studies of chapter 2 the principal difference between the results of analyses of Fourier data and of other data appeared to be in the degree of discrimination between OTUs whilst the pattern of separation of OTUs remained relatively constant. By contrast, the studies of this chapter, which include fossil hominids, have demonstrated differences in both the pattern and the degree of discrimination resulting from analyses of different data. The studies of canonical axes indicated that underlying all analyses there is a common pattern of group relationships which becomes increasingly difficult to discern as successively higher axes are examined.

Earlier, it was suggested that the differences may be the result of either the different description of shape effected by the different methods or of errors in the calculation of Fourier coefficients. In order to gain an insight into the explanation for the differences in result it has been necessary to undertake analyses of different sets of Fourier data and to compare the results of the current studies with those obtained by previous workers.

A reduced set of Fourier components was selected on the basis of their ability to describe the differences between modern groups with a minimum of "noise" and a maximum of discrimination. When the results of the analysis of

this data were compared with the results of the analysis of the fuller Fourier data it was found that there was a considerable degree of agreement.

Some OTUs, particularly those represented by single specimens showed a relatively large shift in apparent morphological affinity and adopted a relationship to other OTUs which is more consistent with the studies of linear and angular measurements and the studies of other workers. From these findings it is concluded that a partial explanation for the differences in result between studies of the first 20 Fourier coefficients and those of linear and angular measurements may well be measurement error (because errors in measurement cannot be "damped" in these OTUs by the calculation of group means).

It was noted from the study of 30 Fourier components, however, that most OTUs still seemed to be in a different position relative to other OTUs when compared to the analyses of angles and dimensions. This suggests that the effects of "noise" are minimal and that the differences between the results obtained from Fourier data and linear and angular measurements reflect real differences in the shape descriptions provided by the different data.

A more detailed comparison of the findings of the analyses of angles and dimensions and of Fourier data with those of other workers was undertaken. It was noted from these that there is some disagreement between the results of studies presented here and those of other workers. The degree of disagreement varies from OTU to OTU, from study to study and from worker to worker. Consistently, the impression that different studies give emphasis to different

aspects of morphology was gained. This seems to be another part of the explanation for the differences between the results of studies of Fourier data and of angles and dimensions.

The results presented in this chapter should serve as a caution to workers who employ phenetic methodologies. The use of (even slightly) different data in analyses employing exactly the same numerical techniques can give rise to very different patterns of phenetic relationships between OTUs. This has been pointed out by several workers (e.g. Wiley, 1981, Ridley, 1986 and many others). The differences in results when different data are used are additional to the differences in patterns of phenetic relationships that result from the use of different phenetic methods (again see Wiley, 1981 and Ridley, 1986).

Why then do the studies of Fourier data disagree to some extent with the studies of angles and dimensions? It has already been noted that the description of a cranium by angles and dimensions is entirely dependent on the identification of landmarks. The anatomy of hominoid crania dictates that useful landmarks are more frequently found in the facial and basal regions. The vault, which may be considerably expanded in more recent *Homo*, presents few such landmarks despite its relative size.

Fourier data, on the other hand, require only one or two landmarks for their derivation and they give equal weighting to all regions of the outline. Thus, the values of Fourier coefficients derived from a cranial outline will be

representative of the whole morphology. The proportionate influence of facial, basal and vault regions will be determined not by the number of identifiable landmarks but by the proportion of the outline which is made up of them. Many differences in result seem to be related to differences in the way in which the data describe neurocranial and viscerocranial morphology.

Why then did the studies of modern groups show a greater degree of agreement between the analyses of different shape measures? The studies of modern groups utilised data from apes and men. The apes are very different from the men whilst within the men and the apes there is a greater degree of general similarity. It is to be expected, therefore, that the large differences in morphology between apes and men are given considerable emphasis (as reflected in large distances between them) in the analyses of all types of data. Conversly, all of the analyses might be expected to agree in indicating considerable similarities within apes and men.

The studies of between-group differences in this chapter contrast with the earlier ones in that the fossils provide a more varied range of morphology. As such the number and types of differences demonstrated between OTUs when different descriptions of morphology are employed are themselves more varied.

## Summary

In this chapter a study is presented which compares the outcome of phenetic studies of fossil hominid crania using Fourier data with that of comparable studies using linear and angular measurements. Earlier studies of the cranial morphology of extant hominoids using these same methods of morphological description resulted in nearly identical patterns of phenetic discrimination irrespective of data type. In contrast, the studies of fossil material have resulted in a reduced (though significant, as judged by matrix correlations) degree of correspondence between the phenetic relationships implied by linear and angular measurements and those implied by Fourier data.

A detailed examination of the results together with a consideration of the findings of phenetic studies of hominid cranial morphology undertaken by previous workers has indicated the following;

a) The studies of Fourier data and those of linear and angular measurements show a significant degree of agreement.

b) There is also a general agreement between these studies and those of previous workers.

c) There are, however, a number of ways in which the phenetic relationships implied by the Fourier data disagree with those implied by linear and angular measurements. These disagreements appear to be related to differences in the morphological descriptions provided by the different data.

d) There also exists some disagreement between the phenetic relationships implied between fossil crania in the studies of previous workers.

It is concluded that:

a) Fourier analysis is not a "simple" substitute for linear and angular measurements.

b) Fourier data describe cranial morphology in a different way to linear and angular dimensions. The former treats each part of the cranial outline as being of equal weight whilst the latter weights anatomical regions according to the number of identifiable landmarks and the measurement protocol. The consequence is that different phenetic patterns emerge.

c) The outcome of a phenetic study is critically dependent upon the measurement (descriptive) procedure which is employed.

# CHAPTER 5

## Cranial form in the Hominoidea.

## Concluding remarks

## General

The principal aim of the work presented in this thesis has been to examine the merits of a number of methods which offer potential in the description of hominoid cranial form. To this end, three studies have been undertaken.

In the first, the phenetic relationships of the crania of extant hominoids were examined using data obtained by a variety of new and more traditional approaches to morphological description. The analysis concentrated on a comparison of the patterns of group dispositions that resulted and on an examination of the ability of the various approaches to allow an accurate determination of the affinities of crania of unknown provenance. The results indicated that there was little difference in the patterns of phenetic relationships obtained although it did appear that the analyses based upon linear and angular measurements and Fourier coefficients provided the widest separation between the groups.

The second study employed linear and angular measurements and Fourier coefficients in an examination of within-group cranial variability. In general the results led to similar conclusions about the patterns of sexual dimorphism in extant hominoid crania and the influence of size on cranial morphology. The analyses of Fourier data differed from those of linear and angular measurements, however, in that purely size related variation was given a smaller weighting relative to morphological variation attributable to other sources.

The third study employed these same two approaches to morphological description in a study of the patterns of cranial variation between certain fossil hominids. By contrast with the first study the methods resulted in different patterns and degrees of discrimination between the groups.

## Overall consideration of results

The results obtained from the different studies show an apparent conflict. From the first it seems that the choice of method for the description of cranial morphology has little influence on the observed pattern of between-group relationships. The second study suggests that this stability in the face of different data is less marked in studies of within-group variation. The third study, however, produces a result which conflicts with that from the first in suggesting that, in some studies, between-group relationships will be influenced by the choice of data.

The hypothesis that the pattern of phenetic relationships which is observed between crania is independent of the method used to describe morphology is clearly falsified.

The reasons why this is so have been considered earlier, they are brought together here, however, so that some general comments and recommendations can be made.

From the descriptions of the methods of morphological description furnished in the introduction to the first study it is evident that the data which they generate differ in a number of ways. Shape factors and Fourier coefficients provide a description which gives every point on the boundary of an outline

equal weighting. This contrasts with linear and angular measurements, indices, and the method of least squares which give disproportionate weighting to those regions where landmarks are plentiful.

In the first study two families of shapes were studied, one represented by the apes, the other by the men. Within both the ape and human groups cranial morphology is broadly similar. Between men and apes, however, marked contrasts in cranial morphology exist. The distance matrices calculated between these extant groups reflect this in indicating small distances between the races of men and between the apes whilst between the men and apes distances are large. The pattern of differences between groups is discontinuous and this emerges irrespective of the method used to describe cranial morphology.

The study of patterns of intra-group variation contrasts with the first study in that more subtle variations in cranial morphology are examined. The results derived from Fourier data contrast with those from linear and angular measurements in the emphasis given to the weighting of morphological differences (such that those related to size are more pronounced on higher principal components). This contrast reflects differences in the descriptions of morphology which are provided by the two sets of data and especially the fact that variations in regions which are relatively unsampled by landmark based data are fully sampled by Fourier data.

In the third study patterns of variation between fossil and extant hominoids were examined. In this study the pattern of relationships was more continuous than in the first, where the pattern of between group phenetic relationships is largely discontinuous. The fossils present a range of cranial morphologies which vary from being largely ape-like to being largely like

anatomically modern *Homo*. Consequently the differences between the descriptions of cranial morphology provided by Fourier data and by linear dimensions and angles were more clearly demonstrated.

In the course of a detailed comparison of the findings of the analyses of linear and angular dimensions with those from Fourier data and those of other workers it was noted that the degree of agreement varied from OTU to OTU, from study to study and from worker to worker. Consistently the impression was gained that Fourier data gave different weighting to the various anatomical regions from that provided by linear and angular measurements. In consequence the observed patterns of phenetic relationships were markedly influenced by the choice of craniometric technique.

## General comments and recommendations

It is clear from the studies presented here that it is feasible to apply numerous methods, some traditional some new, to phenetic studies and that these may lead to different results. It follows that craniometric problems should be precisely defined and the most appropriate methodology chosen for the task at hand.

It is self evident that studies which ask specific questions about specific anatomical regions must rely upon landmarks for the collection of at least some of the data which are to describe those regions. This is because landmarks are needed to define the regions themselves. Furthermore, landmark based data allow specific questions regarding defined anatomical differences to be explored.

By contrast landmark independent methods of morphological description treat the whole cranium as a single object. However the differences which emerge are not readily interpretable in a language familiar to the anatomist. It may be of interest to know that cosine component 2 is weighted more heavily in data calculated from one cranial tracing rather than another but the anatomical meaning of this finding is unclear. On the other hand landmark independent methods offer the advantage that they are easily automated, give even emphasis to all points on an outline and can result in a precise and complete description of a cranial tracing.

From these conclusions it is recommended that:

a) the choice of method for craniometric problems be determined with due regard for the task at hand,

b) the investigator be aware of the potential pitfalls and advantages of each method in furnishing answers to specific questions,

c) the investigator be aware of the fact that the use of different morphological descriptions may give rise to different results.

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# APPENDIX A

## LINEAR AND ANGULAR MEASUREMENTS FROM THE CASTS OF FOSSIL CRANIA

Appendix A

Order of presentation

Cro-Magnon 1
Gamble's Cave 4
Gough's Cave 1
Chancelade 1
Predmost 3
Brno 3
Mladec 1
Fish Hoek 1
Keilor 1
Wadjak 1
Le Moustier 1
La Chapelle-aux-Saints 1
La Ferrassie 1
Monte Circeo 1
Gibraltar 1
Skhul V
Kabwe 1
Steinheim 1
*'Sinanthropus'*
Sangiran 4
KNM-ER 3733
Sts 5
OH 24
OH 5
KNM-ER 406
KNM-ER 1470 (three reconstructions)

## CRO-MAGNON 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 205.00 | |
| 2 | MAX CRANIAL BREADTH | 152.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 135.00 | |
| 4 | AURICULAR HEIGHT | 127.00 | |
| 5 | POSTORBITAL BREADTH | 104.00 | |
| 6 | FRONTAL HEIGHT | 34.00 | |
| 7 | FRONTAL CHORD | 126.00 | |
| 8 | PARIETAL HEIGHT | 24.00 | |
| 9 | PARIETAL CHORD | 118.00 | |
| 10 | OCCIPITAL HEIGHT | 37.00 | |
| 11 | OCCIPITAL CHORD | 103.00 | |
| 12 | FORAMINAL LENGTH | 41.00 | |
| 13 | FORAMINAL BREADTH | 27.00 | |
| 14 | B - L - O | 86.00 | |
| 15 | L - O - BA | 108.00 | |
| 16 | UPPER FACIAL HEIGHT | 66.00 | |
| 17 | PALATAL LENGTH | 59.00 | 1 |
| 18 | PALATAL BREADTH | 40.00 | |
| 19 | NASAL BREADTH | 22.00 | |
| 20 | NASAL HEIGHT | 50.00 | |
| 21 | SUBNASAL HEIGHT | 16.00 | |
| 22 | ORBITAL HEIGHT | 27.00 | |
| 23 | ORBITAL BREADTH | 45.00 | |
| 24 | INFRAORB BREADTH | 62.00 | 2 |
| 25 | BIZYGOMATIC BREADTH | 143.00 | 3 |
| 26 | BASI-INFRAORBITAL LENGTH | 87.00 | |
| 27 | BASI-NASAL LENGTH | 102.00 | |
| 28 | BASI-PROSTHION LENGTH | 107.00 | |
| 29 | BASI-STAPHYLION LENGTH | 47.00 | 1 |
| 30 | BA - N - B | 71.00 | |
| 31 | BA - N - PR | 75.00 | |
| 32 | N - B - L | 103.00 | |
| 33 | N - BA - PR | 37.00 | |
| 34 | O - BA - N | 170.00 | |

Notes

1. Damage to the posterior palate meant that the palatal length and the craniogram tracing in this region were estimated.

2. The presence of encrustations on the face required the estimation of this dimension.

3. Damage to both zygomatic arches required the estimation of this dimension from the general contour of the arches.

## GAMBLE'S CAVE 4

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 190.00 | |
| 2 | MAX CRANIAL BREADTH | 135.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 136.00 | |
| 4 | AURICULAR HEIGHT | 114.00 | |
| 5 | POSTORBITAL BREADTH | 95.00 | |
| 6 | FRONTAL HEIGHT | 29.00 | |
| 7 | FRONTAL CHORD | 110.00 | |
| 8 | PARIETAL HEIGHT | 27.00 | |
| 9 | PARIETAL CHORD | 126.00 | |
| 10 | OCCIPITAL HEIGHT | 24.00 | |
| 11 | OCCIPITAL CHORD | 87.00 | |
| 12 | FORAMINAL LENGTH | 35.00 | |
| 13 | FORAMINAL BREADTH | 26.00 | |
| 14 | B – L – O | 77.00 | |
| 15 | L – O – BA | 148.00 | |
| 16 | UPPER FACIAL HEIGHT | 73.00 | |
| 17 | PALATAL LENGTH | 53.00 | 1 |
| 18 | PALATAL BREADTH | 46.00 | |
| 19 | NASAL BREADTH | 26.00 | |
| 20 | NASAL HEIGHT | 58.00 | |
| 21 | SUBNASAL HEIGHT | 15.00 | |
| 22 | ORBITAL HEIGHT | 41.00 | |
| 23 | ORBITAL BREADTH | 38.00 | |
| 24 | INFRAORB BREADTH | 62.00 | |
| 25 | BIZYGOMATIC BREADTH | 140.00 | |
| 26 | BASI–INFRAORBITAL LENGTH | 88.00 | |
| 27 | BASI–NASAL LENGTH | 106.00 | |
| 28 | BASI–PROSTHION LENGTH | 93.00 | |
| 29 | BASI–STAPHYLION LENGTH | 50.00 | 1 |
| 30 | BA – N – B | 78.00 | |
| 31 | BA – N – PR | 60.00 | |
| 32 | N – B – L | 103.00 | |
| 33 | N – BA – PR | 42.00 | |
| 34 | O – BA – N | 134.00 | |

Notes

1. Damage to posterior palate required the reconstruction of the posterior palate. The positions of Staphylion and of the craniogram tracing were estimated in this region.

## GOUGH'S CAVE 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 195.00 | |
| 2 | MAX CRANIAL BREADTH | 140.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 148.00 | |
| 4 | AURICULAR HEIGHT | 123.00 | |
| 5 | POSTORBITAL BREADTH | 103.00 | |
| 6 | FRONTAL HEIGHT | 27.00 | |
| 7 | FRONTAL CHORD | 120.00 | |
| 8 | PARIETAL HEIGHT | 23.00 | |
| 9 | PARIETAL CHORD | 120.00 | |
| 10 | OCCIPITAL HEIGHT | 27.00 | |
| 11 | OCCIPITAL CHORD | 103.00 | |
| 12 | FORAMINAL LENGTH | 43.00 | |
| 13 | FORAMINAL BREADTH | 35.00 | 1 |
| 14 | B - L - O | 88.00 | |
| 15 | L - O - BA | 123.00 | |
| 16 | UPPER FACIAL HEIGHT | 67.00 | 2 |
| 17 | PALATAL LENGTH | 47.00 | 2,3 |
| 18 | PALATAL BREADTH | 39.00 | |
| 19 | NASAL BREADTH | 28.00 | 4 |
| 20 | NASAL HEIGHT | 49.00 | 5 |
| 21 | SUBNASAL HEIGHT | 17.00 | 2,5 |
| 22 | ORBITAL HEIGHT | 36.00 | |
| 23 | ORBITAL BREADTH | 43.00 | 6 |
| 24 | INFRAORB BREADTH | 55.00 | 4 |
| 25 | BIZYGOMATIC BREADTH | 139.00 | 4 |
| 26 | BASI-INFRAORBITAL LENGTH | 81.00 | 4 |
| 27 | BASI-NASAL LENGTH | 112.00 | |
| 28 | BASI-PROSTHION LENGTH | 96.00 | 2 |
| 29 | BASI-STAPHYLION LENGTH | 50.00 | 3 |
| 30 | BA - N - B | 79.00 | |
| 31 | BA - N - PR | 58.00 | 2 |
| 32 | N - B - L | 106.00 | |
| 33 | N - BA - PR | 36.00 | 2 |
| 34 | O - BA - N | 144.00 | |

Notes

1. Damage to foramen magnum required estimation of this dimension.
2. The position of Prosthion was estimated.
3. The position of Staphylion was estimated.
4. Damage to the left side of the face meant that these dimensions were estimated by reference to the right side.
5. The position of Nariale was estimated.
6. Right orbit damaged, dimension from left.

## CHANCELADE 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 197.00 | |
| 2 | MAX CRANIAL BREADTH | 138.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 153.00 | 1 |
| 4 | AURICULAR HEIGHT | 129.00 | |
| 5 | POSTORBITAL BREADTH | 102.00 | |
| 6 | FRONTAL HEIGHT | 33.00 | 1 |
| 7 | FRONTAL CHORD | 126.00 | 1 |
| 8 | PARIETAL HEIGHT | 28.00 | |
| 9 | PARIETAL CHORD | 122.00 | 1 |
| 10 | OCCIPITAL HEIGHT | 27.00 | |
| 11 | OCCIPITAL CHORD | 99.00 | |
| 12 | FORAMINAL LENGTH | 38.00 | 2 |
| 13 | FORAMINAL BREADTH | 33.00 | 2 |
| 14 | B - L - O | 92.00 | 1 |
| 15 | L - O - BA | 121.00 | 2 |
| 16 | UPPER FACIAL HEIGHT | 70.00 | |
| 17 | PALATAL LENGTH | 52.00 | 3 |
| 18 | PALATAL BREADTH | 41.00 | 4 |
| 19 | NASAL BREADTH | 28.00 | |
| 20 | NASAL HEIGHT | 57.00 | |
| 21 | SUBNASAL HEIGHT | 14.00 | |
| 22 | ORBITAL HEIGHT | 34.00 | |
| 23 | ORBITAL BREADTH | 41.00 | |
| 24 | INFRAORB BREADTH | 49.00 | |
| 25 | BIZYGOMATIC BREADTH | 141.00 | 5 |
| 26 | BASI-INFRAORBITAL LENGTH | 90.00 | 2 |
| 27 | BASI-NASAL LENGTH | 117.00 | 2 |
| 28 | BASI-PROSTHION LENGTH | 99.00 | 2 |
| 29 | BASI-STAPHYLION LENGTH | 47.00 | 2,3 |
| 30 | BA - N - B | 78.00 | 1,2 |
| 31 | BA - N - PR | 58.00 | 2 |
| 32 | N - B - L | 100.00 | 1 |
| 33 | N - BA - PR | 37.00 | 2 |
| 34 | O - BA - N | 148.00 | 2 |

Notes

1. The position of Bregma was estimated on the reconstruction.
2. The region of the foramen magnum was heavily reconstructed. The foraminal breadth is a complete estimate and the position of the basion is also estimated though with confidence.
3. The position of staphylion is estimated though with confidence.
4. The left alveolus is damaged, estimate from right.
5. Estimate based on half measurement from reconstructed right zygomatic arch.

## PREDMOST 3

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 203.00 | |
| 2 | MAX CRANIAL BREADTH | 149.00 | 1 |
| 3 | BASI–BREGMATIC HEIGHT | 136.00 | |
| 4 | AURICULAR HEIGHT | 127.00 | |
| 5 | POSTORBITAL BREADTH | 104.00 | |
| 6 | FRONTAL HEIGHT | 26.00 | |
| 7 | FRONTAL CHORD | 121.00 | |
| 8 | PARIETAL HEIGHT | 25.00 | 2 |
| 9 | PARIETAL CHORD | 119.00 | 2 |
| 10 | OCCIPITAL HEIGHT | 30.00 | 2 |
| 11 | OCCIPITAL CHORD | 99.00 | 2 |
| 12 | FORAMINAL LENGTH | 41.00 | |
| 13 | FORAMINAL BREADTH | 33.00 | 3 |
| 14 | B – L – O | 90.00 | 2 |
| 15 | L – O – BA | 106.00 | 2 |
| 16 | UPPER FACIAL HEIGHT | 76.00 | |
| 17 | PALATAL LENGTH | 57.00 | 4 |
| 18 | PALATAL BREADTH | 43.00 | |
| 19 | NASAL BREADTH | 26.00 | |
| 20 | NASAL HEIGHT | 62.00 | |
| 21 | SUBNASAL HEIGHT | 14.00 | |
| 22 | ORBITAL HEIGHT | 31.00 | |
| 23 | ORBITAL BREADTH | 45.00 | |
| 24 | INFRAORB BREADTH | 57.00 | 5 |
| 25 | BIZYGOMATIC BREADTH | 144.00 | 6 |
| 26 | BASI–INFRAORBITAL LENGTH | 93.00 | |
| 27 | BASI–NASAL LENGTH | 111.00 | |
| 28 | BASI–PROSTHION LENGTH | 114.00 | |
| 29 | BASI–STAPHYLION LENGTH | 59.00 | 4 |
| 30 | BA – N – B | 72.00 | |
| 31 | BA – N – PR | 73.00 | |
| 32 | N – B – L | 105.00 | 2 |
| 33 | N – BA – PR | 40.00 | |
| 34 | O – BA – N | 168.00 | |

Note

1. Right parietal damaged, estimate from left.
2. Position of Lambda is an estimate.
3. Estimated because of damage.
4. The positions of staphylion and the craniogram tracing in this region are estimated.
5. Estimated from half dimension.
6. Right zygomatic arch is missing, estimate from left.

## BRNO 3

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 182.00 | |
| 2 | MAX CRANIAL BREADTH | 127.00 | 1 |
| 3 | BASI–BREGMATIC HEIGHT | 140.00 | |
| 4 | AURICULAR HEIGHT | 116.00 | |
| 5 | POSTORBITAL BREADTH | 92.00 | 2 |
| 6 | FRONTAL HEIGHT | 23.00 | |
| 7 | FRONTAL CHORD | 107.00 | |
| 8 | PARIETAL HEIGHT | 25.00 | |
| 9 | PARIETAL CHORD | 118.00 | |
| 10 | OCCIPITAL HEIGHT | 25.00 | |
| 11 | OCCIPITAL CHORD | 100.00 | |
| 12 | FORAMINAL LENGTH | 34.00 | |
| 13 | FORAMINAL BREADTH | 29.00 | |
| 14 | B – L – O | 87.00 | |
| 15 | L – O – BA | 118.00 | |
| 16 | UPPER FACIAL HEIGHT | 63.00 | |
| 17 | PALATAL LENGTH | 50.00 | 3 |
| 18 | PALATAL BREADTH | 39.00 | |
| 19 | NASAL BREADTH | 30.00 | |
| 20 | NASAL HEIGHT | 51.00 | |
| 21 | SUBNASAL HEIGHT | 13.00 | |
| 22 | ORBITAL HEIGHT | 35.00 | |
| 23 | ORBITAL BREADTH | 40.00 | 4 |
| 24 | INFRAORB BREADTH | 54.00 | 5 |
| 25 | BIZYGOMATIC BREADTH | 122.00 | 6 |
| 26 | BASI–INFRAORBITAL LENGTH | 84.00 | |
| 27 | BASI–NASAL LENGTH | 103.00 | |
| 28 | BASI–PROSTHION LENGTH | 96.00 | |
| 29 | BASI–STAPHYLION LENGTH | 48.00 | 3 |
| 30 | BA – N – B | 85.00 | |
| 31 | BA – N – PR | 66.00 | |
| 32 | N – B – L | 102.00 | |
| 33 | N – BA – PR | 37.00 | |
| 34 | O – BA – N | 149.00 | |

Notes

1. Deficient right parietal, estimate.
2. Damaged temporal fossae, estimate from general contours.
3. The positions of the Staphylion and posterior palate were estimated.
4. Missing parts of nasal bridge, estimated dimension.
5. Estimated from intact right half.
6. Damaged zygomatic arches, estimated from general contours.

## MLADEC 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 199.00 | |
| 2 | MAX CRANIAL BREADTH | 143.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 139.00 | |
| 4 | AURICULAR HEIGHT | 121.00 | |
| 5 | POSTORBITAL BREADTH | 100.00 | |
| 6 | FRONTAL HEIGHT | 32.00 | |
| 7 | FRONTAL CHORD | 116.00 | |
| 8 | PARIETAL HEIGHT | 20.00 | |
| 9 | PARIETAL CHORD | 122.00 | |
| 10 | OCCIPITAL HEIGHT | 32.00 | |
| 11 | OCCIPITAL CHORD | 100.00 | |
| 12 | FORAMINAL LENGTH | 43.00 | |
| 13 | FORAMINAL BREADTH | 30.00 | |
| 14 | B – L – O | 88.00 | |
| 15 | L – O – BA | 111.00 | |
| 16 | UPPER FACIAL HEIGHT | 66.00 | |
| 17 | PALATAL LENGTH | 56.00 | 1 |
| 18 | PALATAL BREADTH | 43.00 | |
| 19 | NASAL BREADTH | 24.00 | |
| 20 | NASAL HEIGHT | 53.00 | |
| 21 | SUBNASAL HEIGHT | 13.00 | |
| 22 | ORBITAL HEIGHT | 31.00 | |
| 23 | ORBITAL BREADTH | 42.00 | |
| 24 | INFRAORB BREADTH | 56.00 | |
| 25 | BIZYGOMATIC BREADTH | 138.00 | 2 |
| 26 | BASI–INFRAORBITAL LENGTH | 87.00 | |
| 27 | BASI–NASAL LENGTH | 103.00 | |
| 28 | BASI–PROSTHION LENGTH | 108.00 | |
| 29 | BASI–STAPHYLION LENGTH | 51.00 | 1 |
| 30 | BA – N – B | 79.00 | |
| 31 | BA – N – PR | 75.00 | |
| 32 | N – B – L | 102.00 | |
| 33 | N – BA – PR | 37.00 | |
| 34 | O – BA – N | 159.00 | |

Notes

1. Positions of Staphylion and palatal outline estimated.

2. Estimated from Right side, left zygomatic arch missing.

## FISH HOEK 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 200.00 | |
| 2 | MAX CRANIAL BREADTH | 151.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 130.00 | |
| 4 | AURICULAR HEIGHT | 117.00 | |
| 5 | POSTORBITAL BREADTH | 106.00 | |
| 6 | FRONTAL HEIGHT | 32.00 | |
| 7 | FRONTAL CHORD | 125.00 | |
| 8 | PARIETAL HEIGHT | 25.00 | |
| 9 | PARIETAL CHORD | 125.00 | |
| 10 | OCCIPITAL HEIGHT | 31.00 | |
| 11 | OCCIPITAL CHORD | 88.00 | |
| 12 | FORAMINAL LENGTH | 39.00 | |
| 13 | FORAMINAL BREADTH | 30.00 | |
| 14 | B – L – O | 76.00 | |
| 15 | L – O – BA | 139.00 | |
| 16 | UPPER FACIAL HEIGHT | 57.00 | |
| 17 | PALATAL LENGTH | 50.00 | |
| 18 | PALATAL BREADTH | 42.00 | |
| 19 | NASAL BREADTH | 25.00 | |
| 20 | NASAL HEIGHT | 43.00 | |
| 21 | SUBNASAL HEIGHT | 15.00 | |
| 22 | ORBITAL HEIGHT | 32.00 | |
| 23 | ORBITAL BREADTH | 38.00 | |
| 24 | INFRAORB BREADTH | 55.00 | |
| 25 | BIZYGOMATIC BREADTH | 132.00 | |
| 26 | BASI–INFRAORBITAL LENGTH | 82.00 | |
| 27 | BASI–NASAL LENGTH | 93.00 | |
| 28 | BASI–PROSTHION LENGTH | 98.00 | |
| 29 | BASI–STAPHYLION LENGTH | 48.00 | |
| 30 | BA – N – B | 71.00 | |
| 31 | BA – N – PR | 78.00 | |
| 32 | N – B – L | 100.00 | |
| 33 | N – BA – PR | 35.00 | |
| 34 | O – BA – N | 154.00 | |

Notes

Cranium largely intact, some damage in the region of the posterior palate though no great problem in estimation of the outline.

## KEILOR 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 202.00 | |
| 2 | MAX CRANIAL BREADTH | 146.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 137.00 | |
| 4 | AURICULAR HEIGHT | 125.00 | |
| 5 | POSTORBITAL BREADTH | 102.00 | |
| 6 | FRONTAL HEIGHT | 23.00 | |
| 7 | FRONTAL CHORD | 112.00 | |
| 8 | PARIETAL HEIGHT | 24.00 | |
| 9 | PARIETAL CHORD | 126.00 | |
| 10 | OCCIPITAL HEIGHT | 34.00 | |
| 11 | OCCIPITAL CHORD | 107.00 | |
| 12 | FORAMINAL LENGTH | 40.00 | |
| 13 | FORAMINAL BREADTH | 32.00 | 1 |
| 14 | B – L – O | 83.00 | |
| 15 | L – O – BA | 112.00 | |
| 16 | UPPER FACIAL HEIGHT | 70.00 | |
| 17 | PALATAL LENGTH | 72.00 | |
| 18 | PALATAL BREADTH | 47.00 | |
| 19 | NASAL BREADTH | 27.00 | |
| 20 | NASAL HEIGHT | 52.00 | |
| 21 | SUBNASAL HEIGHT | 18.00 | |
| 22 | ORBITAL HEIGHT | 30.00 | |
| 23 | ORBITAL BREADTH | 40.00 | |
| 24 | INFRAORB BREADTH | 60.00 | |
| 25 | BIZYGOMATIC BREADTH | 140.00 | 2 |
| 26 | BASI–INFRAORBITAL LENGTH | 93.00 | |
| 27 | BASI–NASAL LENGTH | 110.00 | |
| 28 | BASI–PROSTHION LENGTH | 112.00 | |
| 29 | BASI–STAPHYLION LENGTH | 40.00 | |
| 30 | BA – N – B | 76.00 | |
| 31 | BA – N – PR | 73.00 | |
| 32 | N – B – L | 109.00 | |
| 33 | N – BA – PR | 37.00 | |
| 34 | O – BA – N | 160.00 | |

Notes

1. Foraminal breadth estimated from left half.

2. Estimate from general contours of remaining parts of zygomatic arches.

## WADJAK 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 202.00 | |
| 2 | MAX CRANIAL BREADTH | 152.00 | 1 |
| 3 | BASI–BREGMATIC HEIGHT | 139.00 | 3 |
| 4 | AURICULAR HEIGHT | 121.00 | |
| 5 | POSTORBITAL BREADTH | 99.00 | 2 |
| 6 | FRONTAL HEIGHT | 24.00 | |
| 7 | FRONTAL CHORD | 117.00 | |
| 8 | PARIETAL HEIGHT | 36.00 | |
| 9 | PARIETAL CHORD | 143.00 | |
| 10 | OCCIPITAL HEIGHT | 15.00 | 3 |
| 11 | OCCIPITAL CHORD | 87.00 | 3 |
| 12 | FORAMINAL LENGTH | 35.00 | 3 |
| 13 | FORAMINAL BREADTH | 29.00 | 3 |
| 14 | B – L – O | 79.00 | |
| 15 | L – O – BA | 125.00 | 3 |
| 16 | UPPER FACIAL HEIGHT | 70.00 | 4 |
| 17 | PALATAL LENGTH | 61.00 | 4,5 |
| 18 | PALATAL BREADTH | 44.00 | |
| 19 | NASAL BREADTH | 28.00 | |
| 20 | NASAL HEIGHT | 52.00 | |
| 21 | SUBNASAL HEIGHT | 20.00 | 4 |
| 22 | ORBITAL HEIGHT | 35.00 | |
| 23 | ORBITAL BREADTH | 42.00 | |
| 24 | INFRAORB BREADTH | 65.00 | |
| 25 | BIZYGOMATIC BREADTH | 142.00 | 6 |
| 26 | BASI–INFRAORBITAL LENGTH | 95.00 | 3 |
| 27 | BASI–NASAL LENGTH | 111.00 | 3 |
| 28 | BASI–PROSTHION LENGTH | 113.00 | 3,4 |
| 29 | BASI–STAPHYLION LENGTH | 52.00 | 3,5 |
| 30 | BA – N – B | 75.00 | 3 |
| 31 | BA – N – PR | 73.00 | 3,4 |
| 32 | N – B – L | 96.00 | |
| 33 | N – BA – PR | 36.00 | 3,4 |
| 34 | O – BA – N | 162.00 | 3 |

Notes

1. Both parietals badly damaged, dimension based upon half measurement taken from reconstructed left side.
2. Estimated with regard to the general contours of the damaged temporal fossae.
3. Estimated dimensions because of damage to foramen magnum.
4. Position of Prosthion estimated from general contours.
5. Position of Staphylion estimated from general contours.
6. Positions of zygomatic arches estimated from contours

## LE MOUSTIER 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 205.00 | |
| 2 | MAX CRANIAL BREADTH | 150.00 | 1 |
| 3 | BASI-BREGMATIC HEIGHT | 139.00 | |
| 4 | AURICULAR HEIGHT | 126.00 | |
| 5 | POSTORBITAL BREADTH | 111.00 | 2 |
| 6 | FRONTAL HEIGHT | 21.00 | |
| 7 | FRONTAL CHORD | 108.00 | |
| 8 | PARIETAL HEIGHT | 24.00 | |
| 9 | PARIETAL CHORD | 115.00 | |
| 10 | OCCIPITAL HEIGHT | 33.00 | 3 |
| 11 | OCCIPITAL CHORD | 103.00 | 3 |
| 12 | FORAMINAL LENGTH | 32.00 | 3 |
| 13 | FORAMINAL BREADTH | 29.00 | |
| 14 | B - L - O | 88.00 | 3 |
| 15 | L - O - BA | 110.00 | 3 |
| 16 | UPPER FACIAL HEIGHT | 70.00 | 4 |
| 17 | PALATAL LENGTH | 70.00 | 4 |
| 18 | PALATAL BREADTH | 46.00 | 4 |
| 19 | NASAL BREADTH | 28.00 | 4 |
| 20 | NASAL HEIGHT | 53.00 | 4 |
| 21 | SUBNASAL HEIGHT | 18.00 | 4 |
| 22 | ORBITAL HEIGHT | 42.00 | |
| 23 | ORBITAL BREADTH | 44.00 | |
| 24 | INFRAORB BREADTH | 76.00 | 4 |
| 25 | BIZYGOMATIC BREADTH | 145.00 | 5 |
| 26 | BASI-INFRAORBITAL LENGTH | 110.00 | 4 |
| 27 | BASI-NASAL LENGTH | 127.00 | 4 |
| 28 | BASI-PROSTHION LENGTH | 127.00 | 4 |
| 29 | BASI-STAPHYLION LENGTH | 56.00 | 4 |
| 30 | BA - N - B | 72.00 | 4 |
| 31 | BA - N - PR | 73.00 | 4 |
| 32 | N - B - L | 115.00 | 4 |
| 33 | N - BA - PR | 32.00 | 4 |
| 34 | O - BA - N | 154.00 | 3,4 |

Notes

1. Estimated to account for fragmented left parietal.
2. Estimated with regard to damaged left temporal fossa.
3. Estimated position of Opisthion.
4. The facial skeleton is badly damaged and largely missing, these estimates are taken from the reconstructed cast and estimated where necessary.
5. Both zygomatic arches are damaged, estimate is based upon the general contour.

## LA CHAPELLE-AUX-SAINTS I

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 215.00 | 1 |
| 2 | MAX CRANIAL BREADTH | 160.00 | 1 |
| 3 | BASI-BREGMATIC HEIGHT | 133.00 | 1 |
| 4 | AURICULAR HEIGHT | 114.00 | 1 |
| 5 | POSTORBITAL BREADTH | 111.00 | 1 |
| 6 | FRONTAL HEIGHT | 26.00 | 1 |
| 7 | FRONTAL CHORD | 108.00 | 1 |
| 8 | PARIETAL HEIGHT | 18.00 | 1,2 |
| 9 | PARIETAL CHORD | 115.00 | 1,2 |
| 10 | OCCIPITAL HEIGHT | 35.00 | 1,2 |
| 11 | OCCIPITAL CHORD | 94.00 | 1,2 |
| 12 | FORAMINAL LENGTH | 51.00 | 1 |
| 13 | FORAMINAL BREADTH | 31.00 | 1 |
| 14 | B - L - O | 91.00 | 1,2 |
| 15 | L - O - BA | 110.00 | 1,2 |
| 16 | UPPER FACIAL HEIGHT | 81.00 | |
| 17 | PALATAL LENGTH | 65.00 | 3 |
| 18 | PALATAL BREADTH | 50.00 | 4 |
| 19 | NASAL BREADTH | 34.00 | |
| 20 | NASAL HEIGHT | 61.00 | |
| 21 | SUBNASAL HEIGHT | 20.00 | |
| 22 | ORBITAL HEIGHT | 36.00 | |
| 23 | ORBITAL BREADTH | 47.00 | |
| 24 | INFRAORB BREADTH | 69.00 | |
| 25 | BIZYGOMATIC BREADTH | 148.00 | 5 |
| 26 | BASI-INFRAORBITAL LENGTH | 104.00 | |
| 27 | BASI-NASAL LENGTH | 117.00 | |
| 28 | BASI-PROSTHION LENGTH | 130.00 | |
| 29 | BASI-STAPHYLION LENGTH | 65.00 | 3 |
| 30 | BA - N - B | 73.00 | |
| 31 | BA - N - PR | 80.00 | |
| 32 | N - B - L | 115.00 | 2 |
| 33 | N - BA - PR | 38.00 | |
| 34 | O - BA - N | 151.00 | |

Notes

1. The cranial vault is fragmented but the reconstruction appears adequate.
2. Estimated position of Lambda.
3. Positions of Staphylion and cranial tracing estimated in this region.
4. Estimated from general contour of the alveolus.
5. Right zygomatic arch missing, estimate from left.

## LA FERRASSIE 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 212.00 | |
| 2 | MAX CRANIAL BREADTH | 159.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 136.00 | |
| 4 | AURICULAR HEIGHT | 115.00 | |
| 5 | POSTORBITAL BREADTH | 109.00 | 1 |
| 6 | FRONTAL HEIGHT | 23.00 | |
| 7 | FRONTAL CHORD | 123.00 | |
| 8 | PARIETAL HEIGHT | 23.00 | |
| 9 | PARIETAL CHORD | 114.00 | |
| 10 | OCCIPITAL HEIGHT | 30.00 | |
| 11 | OCCIPITAL CHORD | 97.00 | |
| 12 | FORAMINAL LENGTH | 44.00 | |
| 13 | FORAMINAL BREADTH | 34.00 | |
| 14 | B – L – O | 90.00 | |
| 15 | L – O – BA | 115.00 | |
| 16 | UPPER FACIAL HEIGHT | 92.00 | 2 |
| 17 | PALATAL LENGTH | 59.00 | 2,3 |
| 18 | PALATAL BREADTH | 49.00 | |
| 19 | NASAL BREADTH | 32.00 | 1 |
| 20 | NASAL HEIGHT | 65.00 | |
| 21 | SUBNASAL HEIGHT | 26.00 | 2 |
| 22 | ORBITAL HEIGHT | 37.00 | |
| 23 | ORBITAL BREADTH | 48.00 | 4 |
| 24 | INFRAORB BREADTH | 82.00 | 5 |
| 25 | BIZYGOMATIC BREADTH | 149.00 | 1 |
| 26 | BASI–INFRAORBITAL LENGTH | 96.00 | 5 |
| 27 | BASI–NASAL LENGTH | 123.00 | |
| 28 | BASI–PROSTHION LENGTH | 123.00 | 2 |
| 29 | BASI–STAPHYLION LENGTH | 65.00 | 3 |
| 30 | BA – N – B | 68.00 | |
| 31 | BA – N – PR | 68.00 | 2 |
| 32 | N – B – L | 114.00 | |
| 33 | N – BA – PR | 44.00 | 2 |
| 34 | O – BA – N | 153.00 | |

Notes

1. Cast is reconstructed in these regions, dimensions taken from this reconstruction.
2. Position of Prosthion is estimated.
3. Position of Staphylion is estimated.
4. Estimate from right orbit.
5. Right maxilla damaged estimated from left.

## MONTE CIRCEO 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 205.00 | |
| 2 | MAX CRANIAL BREADTH | 157.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 123.00 | |
| 4 | AURICULAR HEIGHT | 107.00 | |
| 5 | POSTORBITAL BREADTH | 99.00 | 1 |
| 6 | FRONTAL HEIGHT | 20.00 | |
| 7 | FRONTAL CHORD | 118.00 | |
| 8 | PARIETAL HEIGHT | 16.00 | |
| 9 | PARIETAL CHORD | 98.00 | |
| 10 | OCCIPITAL HEIGHT | 43.00 | |
| 11 | OCCIPITAL CHORD | 92.00 | |
| 12 | FORAMINAL LENGTH | 45.00 | 2 |
| 13 | FORAMINAL BREADTH | 29.00 | 2 |
| 14 | B – L – O | 87.00 | 2 |
| 15 | L – O – BA | 120.00 | 2 |
| 16 | UPPER FACIAL HEIGHT | 78.00 | |
| 17 | PALATAL LENGTH | 47.00 | |
| 18 | PALATAL BREADTH | 47.00 | 3 |
| 19 | NASAL BREADTH | 30.00 | 1 |
| 20 | NASAL HEIGHT | 64.00 | |
| 21 | SUBNASAL HEIGHT | 15.00 | |
| 22 | ORBITAL HEIGHT | 36.00 | |
| 23 | ORBITAL BREADTH | 40.00 | |
| 24 | INFRAORB BREADTH | 71.00 | 3 |
| 25 | BIZYGOMATIC BREADTH | 146.00 | 1 |
| 26 | BASI–INFRAORBITAL LENGTH | 84.00 | 3 |
| 27 | BASI–NASAL LENGTH | 104.00 | |
| 28 | BASI–PROSTHION LENGTH | 110.00 | |
| 29 | BASI–STAPHYLION LENGTH | 63.00 | |
| 30 | BA – N – B | 67.00 | |
| 31 | BA – N – PR | 73.00 | |
| 32 | N – B – L | 117.00 | |
| 33 | N – BA – PR | 43.00 | |
| 34 | O – BA – N | 149.00 | 2 |

Notes

The cast which is available in the British Museum (NH) is clearly largely sculptured. All of the measurements are taken from this cast/reconstruction. The reliability of these dimensions as an indicator of the values found in the original is considered elsewhere in this thesis.

1. Estimated from the left side, right side encrusted and damaged.
2. Damaged foramen magnum, estimate.
3. Damaged and encrusted, estimate

## GIBRALTAR 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 193.00 | |
| 2 | MAX CRANIAL BREADTH | 152.00 | 1 |
| 3 | BASI–BREGMATIC HEIGHT | 124.00 | 2 |
| 4 | AURICULAR HEIGHT | 109.00 | 2 |
| 5 | POSTORBITAL BREADTH | 109.00 | 3 |
| 6 | FRONTAL HEIGHT | 25.00 | 2 |
| 7 | FRONTAL CHORD | 114.00 | 2 |
| 8 | PARIETAL HEIGHT | 23.00 | 2 |
| 9 | PARIETAL CHORD | 126.00 | 2 |
| 10 | OCCIPITAL HEIGHT | 23.00 | 4 |
| 11 | OCCIPITAL CHORD | 73.00 | 4 |
| 12 | FORAMINAL LENGTH | 38.00 | 4,5 |
| 13 | FORAMINAL BREADTH | 30.00 | 5 |
| 14 | B – L – O | 82.00 | 2,4 |
| 15 | L – O – BA | 129.00 | 4,5 |
| 16 | UPPER FACIAL HEIGHT | 72.00 | 6 |
| 17 | PALATAL LENGTH | 62.00 | 6 |
| 18 | PALATAL BREADTH | 45.00 | 7 |
| 19 | NASAL BREADTH | 33.00 | |
| 20 | NASAL HEIGHT | 54.00 | |
| 21 | SUBNASAL HEIGHT | 17.00 | 6 |
| 22 | ORBITAL HEIGHT | 39.00 | |
| 23 | ORBITAL BREADTH | 43.00 | |
| 24 | INFRAORB BREADTH | 63.00 | |
| 25 | BIZYGOMATIC BREADTH | 146.00 | 3 |
| 26 | BASI–INFRAORBITAL LENGTH | 89.00 | 3,5 |
| 27 | BASI–NASAL LENGTH | 109.00 | 5 |
| 28 | BASI–PROSTHION LENGTH | 114.00 | 5,6 |
| 29 | BASI–STAPHYLION LENGTH | 52.00 | 5 |
| 30 | BA – N – B | 68.00 | 5,2 |
| 31 | BA – N – PR | 75.00 | 5,6 |
| 32 | N – B – L | 102.00 | 2 |
| 33 | N – BA – PR | 38.00 | 5,6 |
| 34 | O – BA – N | 158.00 | 5 |

Notes

1. Substantial damage to vault, estimate based on right side.
2. Based upon estimated position of bregma.
3. Estimate from right side.
4. Estimated position of opisthion.
5. Damaged in the region of foramen magnum, estimated dimensions.
6. Estimated position of prosthion.
7. Estimated from general contour of alveolus.

## ES-SKHUL V

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 193.00 | 1 |
| 2 | MAX CRANIAL BREADTH | 144.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 126.00 | 2 |
| 4 | AURICULAR HEIGHT | 115.00 | |
| 5 | POSTORBITAL BREADTH | 102.00 | 3 |
| 6 | FRONTAL HEIGHT | 23.00 | 1 |
| 7 | FRONTAL CHORD | 106.00 | 1 |
| 8 | PARIETAL HEIGHT | 26.00 | |
| 9 | PARIETAL CHORD | 123.00 | |
| 10 | OCCIPITAL HEIGHT | 31.00 | |
| 11 | OCCIPITAL CHORD | 94.00 | |
| 12 | FORAMINAL LENGTH | 40.00 | 2 |
| 13 | FORAMINAL BREADTH | 29.00 | 4 |
| 14 | B - L - O | 83.00 | |
| 15 | L - O - BA | 107.00 | 2 |
| 16 | UPPER FACIAL HEIGHT | 75.00 | 5 |
| 17 | PALATAL LENGTH | 63.00 | 5 |
| 18 | PALATAL BREADTH | 48.00 | |
| 19 | NASAL BREADTH | 31.00 | 5 |
| 20 | NASAL HEIGHT | 55.00 | 5 |
| 21 | SUBNASAL HEIGHT | 19.00 | 5 |
| 22 | ORBITAL HEIGHT | 31.00 | 5 |
| 23 | ORBITAL BREADTH | 47.00 | 5 |
| 24 | INFRAORB BREADTH | 62.00 | 5 |
| 25 | BIZYGOMATIC BREADTH | 145.00 | |
| 26 | BASI-INFRAORBITAL LENGTH | 83.00 | 2,5 |
| 27 | BASI-NASAL LENGTH | 96.00 | 2,5 |
| 28 | BASI-PROSTHION LENGTH | 112.00 | 2,5 |
| 29 | BASI-STAPHYLION LENGTH | 50.00 | 2 |
| 30 | BA - N - B | 76.00 | 2,5 |
| 31 | BA - N - PR | 81.00 | 2,5 |
| 32 | N - B - L | 102.00 | |
| 33 | N - BA - PR | 41.00 | 2,5 |
| 34 | O - BA - N | 170.00 | 2,5 |

Notes

1. Position of glabella taken from reconstructed cast.
2. Based upon reconstructed position of basion.
3. Damaged left temporal fossa, estimated from reconstruction.
4. Estimated from left.
5. Based upon the facial reconstruction.

## KABWE 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 211.00 | 1 |
| 2 | MAX CRANIAL BREADTH | 148.00 | 2 |
| 3 | BASI–BREGMATIC HEIGHT | 133.00 | |
| 4 | AURICULAR HEIGHT | 115.00 | 2 |
| 5 | POSTORBITAL BREADTH | 101.00 | |
| 6 | FRONTAL HEIGHT | 21.00 | |
| 7 | FRONTAL CHORD | 124.00 | |
| 8 | PARIETAL HEIGHT | 17.00 | |
| 9 | PARIETAL CHORD | 114.00 | |
| 10 | OCCIPITAL HEIGHT | 31.00 | |
| 11 | OCCIPITAL CHORD | 90.00 | |
| 12 | FORAMINAL LENGTH | 43.00 | |
| 13 | FORAMINAL BREADTH | 39.00 | |
| 14 | B – L – O | 88.00 | |
| 15 | L – O – BA | 122.00 | |
| 16 | UPPER FACIAL HEIGHT | 89.00 | |
| 17 | PALATAL LENGTH | 67.00 | |
| 18 | PALATAL BREADTH | 50.00 | |
| 19 | NASAL BREADTH | 32.00 | |
| 20 | NASAL HEIGHT | 64.00 | |
| 21 | SUBNASAL HEIGHT | 26.00 | |
| 22 | ORBITAL HEIGHT | 40.00 | |
| 23 | ORBITAL BREADTH | 50.00 | |
| 24 | INFRAORB BREADTH | 73.00 | |
| 25 | BIZYGOMATIC BREADTH | 149.00 | 3 |
| 26 | BASI–INFRAORBITAL LENGTH | 90.00 | |
| 27 | BASI–NASAL LENGTH | 113.00 | |
| 28 | BASI–PROSTHION LENGTH | 119.00 | |
| 29 | BASI–STAPHYLION LENGTH | 54.00 | |
| 30 | BA – N – B | 68.00 | |
| 31 | BA – N – PR | 71.00 | |
| 32 | N – B – L | 109.00 | |
| 33 | N – BA – PR | 45.00 | |
| 34 | O – BA – N | 153.00 | |

Notes

1. Estimate includes reconstructed opisthocranion.
2. Estimate includes reconstructed right half.
3. Estimate from left side.

## STEINHEIM 1

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 186.00 | |
| 2 | MAX CRANIAL BREADTH | 134.00 | 1 |
| 3 | BASI–BREGMATIC HEIGHT | 115.00 | |
| 4 | AURICULAR HEIGHT | 109.00 | |
| 5 | POSTORBITAL BREADTH | 97.00 | 1 |
| 6 | FRONTAL HEIGHT | 24.00 | |
| 7 | FRONTAL CHORD | 97.00 | |
| 8 | PARIETAL HEIGHT | 15.00 | |
| 9 | PARIETAL CHORD | 96.00 | |
| 10 | OCCIPITAL HEIGHT | 40.00 | 2 |
| 11 | OCCIPITAL CHORD | 94.00 | 2 |
| 12 | FORAMINAL LENGTH | 34.00 | 2 |
| 13 | FORAMINAL BREADTH | 27.00 | 2 |
| 14 | B – L – O | 86.00 | 2 |
| 15 | L – O – BA | 107.00 | 2 |
| 16 | UPPER FACIAL HEIGHT | 69.00 | 3 |
| 17 | PALATAL LENGTH | 65.00 | 3 |
| 18 | PALATAL BREADTH | 42.00 | 1,3 |
| 19 | NASAL BREADTH | 31.00 | 1,3 |
| 20 | NASAL HEIGHT | 50.00 | 3 |
| 21 | SUBNASAL HEIGHT | 17.00 | 3 |
| 22 | ORBITAL HEIGHT | 32.00 | 1,3 |
| 23 | ORBITAL BREADTH | 37.00 | 1,3 |
| 24 | INFRAORB BREADTH | 61.00 | 1,3 |
| 25 | BIZYGOMATIC BREADTH | 128.00 | 3,4 |
| 26 | BASI–INFRAORBITAL LENGTH | 79.00 | 1 |
| 27 | BASI–NASAL LENGTH | 93.00 | |
| 28 | BASI–PROSTHION LENGTH | 107.00 | 1,3 |
| 29 | BASI–STAPHYLION LENGTH | 43.00 | |
| 30 | BA – N – B | 75.00 | |
| 31 | BA – N – PR | 83.00 | 1,3 |
| 32 | N – B – L | 112.00 | |
| 33 | N – BA – PR | 38.00 | 1,3 |
| 34 | O – BA – N | 160.00 | 2 |

Notes

This specimen is badly damaged and may be distorted. All interpretations of the results based upon it should bear this damage in mind.

1. Estimated from right side.
2. Damage in region of foramen magnum, estimated breadth and position of opisthion.
3. Estimate attempts to account for facial distortion and damage
4. Estimate from right, zygomatic arch missing, based on general contour.

## *"SINANTHROPUS"*

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 194.00 | |
| 2 | MAX CRANIAL BREADTH | 143.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 121.00 | |
| 4 | AURICULAR HEIGHT | 99.00 | |
| 5 | POSTORBITAL BREADTH | 95.00 | |
| 6 | FRONTAL HEIGHT | 21.00 | |
| 7 | FRONTAL CHORD | 110.00 | |
| 8 | PARIETAL HEIGHT | 17.00 | |
| 9 | PARIETAL CHORD | 114.00 | |
| 10 | OCCIPITAL HEIGHT | 19.00 | |
| 11 | OCCIPITAL CHORD | 77.00 | |
| 12 | FORAMINAL LENGTH | 27.00 | |
| 13 | FORAMINAL BREADTH | 24.00 | |
| 14 | B – L – O | 85.00 | |
| 15 | L – O – BA | 119.00 | |
| 16 | UPPER FACIAL HEIGHT | 76.00 | |
| 17 | PALATAL LENGTH | 60.00 | |
| 18 | PALATAL BREADTH | 42.00 | |
| 19 | NASAL BREADTH | 30.00 | |
| 20 | NASAL HEIGHT | 54.00 | |
| 21 | SUBNASAL HEIGHT | 23.00 | |
| 22 | ORBITAL HEIGHT | 34.00 | |
| 23 | ORBITAL BREADTH | 43.00 | |
| 24 | INFRAORB BREADTH | 49.00 | |
| 25 | BIZYGOMATIC BREADTH | 148.00 | |
| 26 | BASI–INFRAORBITAL LENGTH | 105.00 | |
| 27 | BASI–NASAL LENGTH | 126.00 | |
| 28 | BASI–PROSTHION LENGTH | 131.00 | |
| 29 | BASI–STAPHYLION LENGTH | 71.00 | |
| 30 | BA – N – B | 61.00 | |
| 31 | BA – N – PR | 77.00 | |
| 32 | N – B – L | 112.00 | |
| 33 | N – BA – PR | 34.00 | |
| 34 | O – BA – N | 162.00 | |

Notes

The cast is of a sculpted reconstruction (Weidenreich, 1937). All measurements were taken from this reconstruction.

## SANGIRAN 4

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 200.00 | 1 |
| 2 | MAX CRANIAL BREADTH | 157.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 102.00 | 1 |
| 4 | AURICULAR HEIGHT | 94.00 | 1 |
| 5 | POSTORBITAL BREADTH | 101.00 | 1 |
| 6 | FRONTAL HEIGHT | 20.00 | 1 |
| 7 | FRONTAL CHORD | 107.00 | 1 |
| 8 | PARIETAL HEIGHT | 12.00 | 1 |
| 9 | PARIETAL CHORD | 93.00 | 1 |
| 10 | OCCIPITAL HEIGHT | 34.00 | |
| 11 | OCCIPITAL CHORD | 76.00 | |
| 12 | FORAMINAL LENGTH | 37.00 | 1 |
| 13 | FORAMINAL BREADTH | 33.00 | |
| 14 | B – L – O | 78.00 | 1 |
| 15 | L – O – BA | 130.00 | 1 |
| 16 | UPPER FACIAL HEIGHT | 76.00 | 1 |
| 17 | PALATAL LENGTH | 84.00 | 1 |
| 18 | PALATAL BREADTH | 60.00 | |
| 19 | NASAL BREADTH | 35.00 | 1 |
| 20 | NASAL HEIGHT | 48.00 | 1 |
| 21 | SUBNASAL HEIGHT | 31.00 | 1 |
| 22 | ORBITAL HEIGHT | 34.00 | 1 |
| 23 | ORBITAL BREADTH | 44.00 | 1 |
| 24 | INFRAORB BREADTH | 72.00 | 1 |
| 25 | BIZYGOMATIC BREADTH | 169.00 | 1 |
| 26 | BASI–INFRAORBITAL LENGTH | 96.00 | 1 |
| 27 | BASI–NASAL LENGTH | 104.00 | 1 |
| 28 | BASI–PROSTHION LENGTH | 125.00 | 1 |
| 29 | BASI–STAPHYLION LENGTH | 43.00 | 1 |
| 30 | BA – N – B | 58.00 | 1 |
| 31 | BA – N – PR | 86.00 | 1 |
| 32 | N – B – L | 124.00 | 1 |
| 33 | N – BA – PR | 38.00 | 1 |
| 34 | O – BA – N | 151.00 | 1 |

Notes

1. This specimen consists of a calotte and palate. The intervening facial and neurocranial elements have been reconstructed in plaster by Weidenreich (1941a). The positions of Bregma, Basion, Staphylion, Nariale, Nasion, Glabella, the zygomatic arches, and the major part of the face are taken from the reconstruction. All of the measurements taken between these landmarks and in these regions should be regarded as estimates.

## KNM-ER 3733

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 178.00 | |
| 2 | MAX CRANIAL BREADTH | 137.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 105.00 | 1 |
| 4 | AURICULAR HEIGHT | 93.00 | |
| 5 | POSTORBITAL BREADTH | 92.00 | |
| 6 | FRONTAL HEIGHT | 16.00 | 1 |
| 7 | FRONTAL CHORD | 99.00 | 1 |
| 8 | PARIETAL HEIGHT | 17.00 | 1 |
| 9 | PARIETAL CHORD | 86.00 | 1 |
| 10 | OCCIPITAL HEIGHT | 34.00 | |
| 11 | OCCIPITAL CHORD | 86.00 | |
| 12 | FORAMINAL LENGTH | 32.00 | |
| 13 | FORAMINAL BREADTH | 32.00 | 2 |
| 14 | B - L - O | 95.00 | 1 |
| 15 | L - O - BA | 90.00 | |
| 16 | UPPER FACIAL HEIGHT | 78.00 | 3 |
| 17 | PALATAL LENGTH | 57.00 | 3,8 |
| 18 | PALATAL BREADTH | 33.00 | 4 |
| 19 | NASAL BREADTH | 35.00 | 5 |
| 20 | NASAL HEIGHT | 50.00 | |
| 21 | SUBNASAL HEIGHT | 28.00 | 3 |
| 22 | ORBITAL HEIGHT | 37.00 | 6 |
| 23 | ORBITAL BREADTH | 43.00 | 6 |
| 24 | INFRAORB BREADTH | 73.00 | 7 |
| 25 | BIZYGOMATIC BREADTH | 136.00 | 5 |
| 26 | BASI-INFRAORBITAL LENGTH | 81.00 | 7 |
| 27 | BASI-NASAL LENGTH | 99.00 | |
| 28 | BASI-PROSTHION LENGTH | 115.00 | 3 |
| 29 | BASI-STAPHYLION LENGTH | 57.00 | 8 |
| 30 | BA - N - B | 63.00 | 1 |
| 31 | BA - N - PR | 81.00 | 3 |
| 32 | N - B - L | 116.00 | 1 |
| 33 | N - BA - PR | 41.00 | 3 |
| 34 | O - BA - N | 175.00 | |

Notes

1. Estimated position of Bregma
2. ? distorted.
3. Prosthion position unclear - estimated.
4. Estimate accounts for damage to alveolus.
5. Estimate from left
6. Estimate to account for damage to orbits.
7. Estimate
8. Staphylion position estimated

Sts 5

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 147.00 | |
| 2 | MAX CRANIAL BREADTH | 100.00 | |
| 3 | BASI–BREGMATIC HEIGHT | 105.00 | |
| 4 | AURICULAR HEIGHT | 74.00 | |
| 5 | POSTORBITAL BREADTH | 66.00 | |
| 6 | FRONTAL HEIGHT | 18.00 | |
| 7 | FRONTAL CHORD | 76.00 | |
| 8 | PARIETAL HEIGHT | 15.00 | |
| 9 | PARIETAL CHORD | 84.00 | |
| 10 | OCCIPITAL HEIGHT | 16.00 | |
| 11 | OCCIPITAL CHORD | 57.00 | |
| 12 | FORAMINAL LENGTH | 30.00 | |
| 13 | FORAMINAL BREADTH | 24.00 | |
| 14 | B – L – O | 100.00 | |
| 15 | L – O – BA | 130.00 | |
| 16 | UPPER FACIAL HEIGHT | 71.00 | |
| 17 | PALATAL LENGTH | 72.00 | |
| 18 | PALATAL BREADTH | 38.00 | |
| 19 | NASAL BREADTH | 25.00 | |
| 20 | NASAL HEIGHT | 43.00 | |
| 21 | SUBNASAL HEIGHT | 29.00 | |
| 22 | ORBITAL HEIGHT | 29.00 | |
| 23 | ORBITAL BREADTH | 37.00 | |
| 24 | INFRAORB BREADTH | 46.00 | |
| 25 | BIZYGOMATIC BREADTH | 126.00 | |
| 26 | BASI–INFRAORBITAL LENGTH | 87.00 | |
| 27 | BASI–NASAL LENGTH | 92.00 | |
| 28 | BASI–PROSTHION LENGTH | 126.00 | |
| 29 | BASI–STAPHYLION LENGTH | 53.00 | |
| 30 | BA – N – B | 74.00 | |
| 31 | BA – N – PR | 99.00 | |
| 32 | N – B – L | 106.00 | |
| 33 | N – BA – PR | 34.00 | |
| 34 | O – BA – N | 134.00 | |

Notes

Relatively complete. Minimal reconstruction of posterior palate, posterior part of nasal septum, left vault and prosthion.

## OH 24

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G–OP) | 145.00 | 1 |
| 2 | MAX CRANIAL BREADTH | 118.00 | 1 |
| 3 | BASI–BREGMATIC HEIGHT | 89.00 | 1 |
| 4 | AURICULAR HEIGHT | 74.00 | 1 |
| 5 | POSTORBITAL BREADTH | 72.00 | 2 |
| 6 | FRONTAL HEIGHT | 15.00 | 1 |
| 7 | FRONTAL CHORD | 76.00 | 1 |
| 8 | PARIETAL HEIGHT | 16.00 | 1 |
| 9 | PARIETAL CHORD | 93.00 | 1 |
| 10 | OCCIPITAL HEIGHT | 21.00 | 1 |
| 11 | OCCIPITAL CHORD | 69.00 | 1 |
| 12 | FORAMINAL LENGTH | 29.00 | 1 |
| 13 | FORAMINAL BREADTH | 25.00 | 1 |
| 14 | B – L – O | 66.00 | 1 |
| 15 | L – O – BA | 149.00 | 1 |
| 16 | UPPER FACIAL HEIGHT | 60.00 | 3 |
| 17 | PALATAL LENGTH | 54.00 | 3 |
| 18 | PALATAL BREADTH | 36.00 | |
| 19 | NASAL BREADTH | 25.00 | |
| 20 | NASAL HEIGHT | 39.00 | |
| 21 | SUBNASAL HEIGHT | 23.00 | 3 |
| 22 | ORBITAL HEIGHT | 30.00 | |
| 23 | ORBITAL BREADTH | 35.00 | 4 |
| 24 | INFRAORB BREADTH | 50.00 | 4 |
| 25 | BIZYGOMATIC BREADTH | 114.00 | 5 |
| 26 | BASI–INFRAORBITAL LENGTH | 64.00 | 4 |
| 27 | BASI–NASAL LENGTH | 66.00 | |
| 28 | BASI–PROSTHION LENGTH | 92.00 | 3 |
| 29 | BASI–STAPHYLION LENGTH | 39.00 | |
| 30 | BA – N – B | 77.00 | 1 |
| 31 | BA – N – PR | 94.00 | 3 |
| 32 | N – B – L | 110.00 | 1 |
| 33 | N – BA – PR | 40.00 | 3 |
| 34 | O – BA – N | 140.00 | |

Notes

This cranium was fragmented and badly crushed when found (Leakey, 1969). The cast which was measured is taken from the reconstruction of Leakey, Clarke and Leakey (1971).

1. Estimate based upon the reconstruction, missing fragments.
2. Temporal fossae damaged bilaterally.
3. The position of prosthion is estimated.
4. Estimate based upon right side/half dimension.
5. Estimate from contours, zygomatic arches missing.

## OH 5

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 166.00 | |
| 2 | MAX CRANIAL BREADTH | 120.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 99.00 | 1 |
| 4 | AURICULAR HEIGHT | 77.00 | 1 |
| 5 | POSTORBITAL BREADTH | 67.00 | 2 |
| 6 | FRONTAL HEIGHT | 10.00 | 1 |
| 7 | FRONTAL CHORD | 89.00 | 1 |
| 8 | PARIETAL HEIGHT | 21.00 | 1 |
| 9 | PARIETAL CHORD | 97.00 | 1 |
| 10 | OCCIPITAL HEIGHT | 21.00 | |
| 11 | OCCIPITAL CHORD | 62.00 | |
| 12 | FORAMINAL LENGTH | 28.00 | |
| 13 | FORAMINAL BREADTH | 25.00 | |
| 14 | B - L - O | 84.00 | 1 |
| 15 | L - O - BA | 122.00 | |
| 16 | UPPER FACIAL HEIGHT | 94.00 | |
| 17 | PALATAL LENGTH | 84.00 | |
| 18 | PALATAL BREADTH | 41.00 | |
| 19 | NASAL BREADTH | 34.00 | 3 |
| 20 | NASAL HEIGHT | 63.00 | |
| 21 | SUBNASAL HEIGHT | 34.00 | |
| 22 | ORBITAL HEIGHT | 35.00 | 4 |
| 23 | ORBITAL BREADTH | 40.00 | 4 |
| 24 | INFRAORB BREADTH | 60.00 | 4 |
| 25 | BIZYGOMATIC BREADTH | 162.00 | 4 |
| 26 | BASI-INFRAORBITAL LENGTH | 108.00 | 4 |
| 27 | BASI-NASAL LENGTH | 105.00 | |
| 28 | BASI-PROSTHION LENGTH | 138.00 | |
| 29 | BASI-STAPHYLION LENGTH | 57.00 | |
| 30 | BA - N - B | 61.00 | 1 |
| 31 | BA - N - PR | 88.00 | |
| 32 | N - B - L | 115.00 | 1 |
| 33 | N - BA - PR | 43.00 | |
| 34 | O - BA - N | 157.00 | |

Notes

1. Estimated position of Bregma.
2. Damaged temporal fossae.
3. Estimate accounting for damaged maxillae.
4. Estimate taken from reconstruction.

## KNM-ER 406

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 158.00 | |
| 2 | MAX CRANIAL BREADTH | 111.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 105.00 | |
| 4 | AURICULAR HEIGHT | 76.00 | |
| 5 | POSTORBITAL BREADTH | 66.00 | 1 |
| 6 | FRONTAL HEIGHT | 12.00 | |
| 7 | FRONTAL CHORD | 93.00 | |
| 8 | PARIETAL HEIGHT | 15.00 | |
| 9 | PARIETAL CHORD | 84.00 | |
| 10 | OCCIPITAL HEIGHT | 12.00 | |
| 11 | OCCIPITAL CHORD | 59.00 | |
| 12 | FORAMINAL LENGTH | 34.00 | |
| 13 | FORAMINAL BREADTH | 32.00 | |
| 14 | B - L - O | 97.00 | |
| 15 | L - O - BA | 125.00 | |
| 16 | UPPER FACIAL HEIGHT | 77.00 | 2 |
| 17 | PALATAL LENGTH | 66.00 | 2 |
| 18 | PALATAL BREADTH | 48.00 | 3 |
| 19 | NASAL BREADTH | 28.00 | |
| 20 | NASAL HEIGHT | 52.00 | |
| 21 | SUBNASAL HEIGHT | 27.00 | 2 |
| 22 | ORBITAL HEIGHT | 36.00 | |
| 23 | ORBITAL BREADTH | 37.00 | |
| 24 | INFRAORB BREADTH | 68.00 | |
| 25 | BIZYGOMATIC BREADTH | 175.00 | 1 |
| 26 | BASI-INFRAORBITAL LENGTH | 100.00 | |
| 27 | BASI-NASAL LENGTH | 104.00 | |
| 28 | BASI-PROSTHION LENGTH | 130.00 | 2 |
| 29 | BASI-STAPHYLION LENGTH | 64.00 | |
| 30 | BA - N - B | 64.00 | |
| 31 | BA - N - PR | 90.00 | 2 |
| 32 | N - B - L | 114.00 | |
| 33 | N - BA - PR | 37.00 | 2 |
| 34 | O - BA - N | 140.00 | |

Notes

1. Left temporal fossa filled with mineral.
2. Estimated position of prosthion.
3. Both alveoli encrusted, estimate.

## KNM-ER 1470 - FACE ANTERIOR

| | | |
|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 171.00 |
| 2 | MAX CRANIAL BREADTH | 114.00 |
| 3 | BASI-BREGMATIC HEIGHT | 123.00 |
| 4 | AURICULAR HEIGHT | 96.00 |
| 5 | POSTORBITAL BREADTH | 77.00 |
| 6 | FRONTAL HEIGHT | 16.00 |
| 7 | FRONTAL CHORD | 93.00 |
| 8 | PARIETAL HEIGHT | 14.00 |
| 9 | PARIETAL CHORD | 97.00 |
| 10 | OCCIPITAL HEIGHT | 16.00 |
| 11 | OCCIPITAL CHORD | 65.00 |
| 12 | FORAMINAL LENGTH | 32.00 |
| 13 | FORAMINAL BREADTH | 28.00 |
| 14 | B - L - O | 98.00 |
| 15 | L - O - BA | 130.00 |
| 16 | UPPER FACIAL HEIGHT | 92.00 |
| 17 | PALATAL LENGTH | 60.00 |
| 18 | PALATAL BREADTH | 44.00 |
| 19 | NASAL BREADTH | 27.00 |
| 20 | NASAL HEIGHT | 58.00 |
| 21 | SUBNASAL HEIGHT | 35.00 |
| 22 | ORBITAL HEIGHT | 38.00 |
| 23 | ORBITAL BREADTH | 41.00 |
| 24 | INFRAORB BREADTH | 52.00 |
| 25 | BIZYGOMATIC BREADTH | 132.00 |
| 26 | BASI-INFRAORBITAL LENGTH | 110.00 |
| 27 | BASI-NASAL LENGTH | 126.00 |
| 28 | BASI-PROSTHION LENGTH | 126.00 |
| 29 | BASI-STAPHYLION LENGTH | 65.00 |
| 30 | BA - N - B | 67.00 |
| 31 | BA - N - PR | 69.00 |
| 32 | N - B - L | 115.00 |
| 33 | N - BA - PR | 43.00 |
| 34 | O - BA - N | 130.00 |

Notes

This fossil is badly fragmented and lacks many parts of the cranial base, vault, face and palate. A large number of measurements are estimates. For details see the notes relating to the "intermediate" reconstruction, overleaf.

## KNM-ER 1470 - FACE INTERMEDIATE

| | | | Notes |
|---|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 171.00 | |
| 2 | MAX CRANIAL BREADTH | 118.00 | |
| 3 | BASI-BREGMATIC HEIGHT | 114.00 | 1 |
| 4 | AURICULAR HEIGHT | 95.00 | 2 |
| 5 | POSTORBITAL BREADTH | 78.00 | |
| 6 | FRONTAL HEIGHT | 14.00 | |
| 7 | FRONTAL CHORD | 92.00 | |
| 8 | PARIETAL HEIGHT | 14.00 | |
| 9 | PARIETAL CHORD | 100.00 | |
| 10 | OCCIPITAL HEIGHT | 18.00 | 1 |
| 11 | OCCIPITAL CHORD | 70.00 | 1 |
| 12 | FORAMINAL LENGTH | 32.00 | 1 |
| 13 | FORAMINAL BREADTH | 28.00 | 1 |
| 14 | B - L - O | 93.00 | 1 |
| 15 | L - O - BA | 117.00 | 1 |
| 16 | UPPER FACIAL HEIGHT | 91.00 | |
| 17 | PALATAL LENGTH | 59.00 | 3 |
| 18 | PALATAL BREADTH | 43.00 | 3 |
| 19 | NASAL BREADTH | 28.00 | 3 |
| 20 | NASAL HEIGHT | 56.00 | |
| 21 | SUBNASAL HEIGHT | 37.00 | |
| 22 | ORBITAL HEIGHT | 38.00 | 4 |
| 23 | ORBITAL BREADTH | 42.00 | 4 |
| 24 | INFRAORB BREADTH | 52.00 | 3 |
| 25 | BIZYGOMATIC BREADTH | 132.00 | 3 |
| 26 | BASI-INFRAORBITAL LENGTH | 100.00 | 1,3 |
| 27 | BASI-NASAL LENGTH | 113.00 | 1 |
| 28 | BASI-PROSTHION LENGTH | 116.00 | 1 |
| 29 | BASI-STAPHYLION LENGTH | 58.00 | 1,3 |
| 30 | BA - N - B | 67.00 | 1 |
| 31 | BA - N - PR | 68.00 | 1 |
| 32 | N - B - L | 114.00 | |
| 33 | N - BA - PR | 47.00 | 1 |
| 34 | O - BA - N | 151.00 | 1 |

Notes

1. Foraminal region missing, estimated position of boundaries.
2. Estimated position of porion.
3. Estimated by Professor E.H. Ashton, checked for anatomical sense by myself.
4. Taken from reconstruction

## KNM-ER 1470 - FACE POSTERIOR

| | | |
|---|---|---|
| 1 | MAX. LENGTH (G-OP) | 170.00 |
| 2 | MAX CRANIAL BREADTH | 117.00 |
| 3 | BASI-BREGMATIC HEIGHT | 106.00 |
| 4 | AURICULAR HEIGHT | 93.00 |
| 5 | POSTORBITAL BREADTH | 77.00 |
| 6 | FRONTAL HEIGHT | 16.00 |
| 7 | FRONTAL CHORD | 91.00 |
| 8 | PARIETAL HEIGHT | 16.00 |
| 9 | PARIETAL CHORD | 97.00 |
| 10 | OCCIPITAL HEIGHT | 23.00 |
| 11 | OCCIPITAL CHORD | 71.00 |
| 12 | FORAMINAL LENGTH | 32.00 |
| 13 | FORAMINAL BREADTH | 28.00 |
| 14 | B - L - O | 86.00 |
| 15 | L - O - BA | 121.00 |
| 16 | UPPER FACIAL HEIGHT | 90.00 |
| 17 | PALATAL LENGTH | 53.00 |
| 18 | PALATAL BREADTH | 43.00 |
| 19 | NASAL BREADTH | 27.00 |
| 20 | NASAL HEIGHT | 56.00 |
| 21 | SUBNASAL HEIGHT | 36.00 |
| 22 | ORBITAL HEIGHT | 38.00 |
| 23 | ORBITAL BREADTH | 40.00 |
| 24 | INFRAORB BREADTH | 54.00 |
| 25 | BIZYGOMATIC BREADTH | 133.00 |
| 26 | BASI-INFRAORBITAL LENGTH | 92.00 |
| 27 | BASI-NASAL LENGTH | 103.00 |
| 28 | BASI-PROSTHION LENGTH | 110.00 |
| 29 | BASI-STAPHYLION LENGTH | 60.00 |
| 30 | BA - N - B | 66.00 |
| 31 | BA - N - PR | 70.00 |
| 32 | N - B - L | 116.00 |
| 33 | N - BA - PR | 50.00 |
| 34 | O - BA - N | 153.00 |

Notes

See notes relating to previous reconstructions.

# APPENDIX B

## THE IDENTIFICATION OF FOSSIL GROUPS FOR CANONICAL ANALYSIS

# INTRODUCTION

## The Identification of suitable groups for Canonical Analysis

In this appendix, I outline the problems associated with the identification of suitable groups of fossil crania for the canonical analyses of chapter 4. A series of studies is presented which allow consideration of the validity of the chosen groups and the consideration of patterns of morphological variation within them.

### Mahalanobis' distances and Canonical Analysis

Mahalanobis' $D^2$ (Mahalanobis, 1936) is widely used in numerical taxonomy (see the review of previous multivariate studies of cranial form in hominids, chapter 4). The Mahalanobis distance, unlike Euclidean distance, is free of distortions consequent upon character correlations. Mahalanobis' distances, however, can only be derived from data taken from populations and the calculation employs "knowledge" of intra OTU variation.

The Mahalanobis distance is closely related to discriminant analysis as first described by Fisher (1936). The space of the original data is transformed into a new space in which the axes are stretched and skewed in order to produce hyperspherical clusters of OTUs. The skewing corrects for correlations and the stretching is in inverse proportion to the standard deviation of the groups on each axis (resulting in an equalisation of the "scale" of each axis). Distances measured between OTUs in this space are independent of correlations between

the original variables and the space is scaled such that the distances between OTUs are expressed in pooled within-group standard deviation units. The distance between an individual and a group centroid relates to the likelihood of its being a member of that taxon.

It follows that a requirement for the calculation of $D^2$ is that the groups in the analysis have identical or very similar variances on each of the original dimensions. If this is not the case then some transformation of the data (see Sokal and Rohlf, 1969) may provide an adequate correction.

Gower (1966) has described a technique, principal coordinate analysis, for deriving an ordination of group dispositions from a distance matrix without reference to the original data. When applied to a Euclidean distance matrix the resultant principal coordinates are equivalent to principal components. When applied to a Mahalanobis' distance matrix the principal coordinates are effectively canonical variates. In this way canonical analysis is closely allied to Mahalanobis' $D^2$.

The Mahalanobis distance can be calculated only when groups of organisms have already been defined. This is potentially a serious problem, it effectively limits the applicability of the Mahalanobis' distances and canonical analysis to situations where higher taxonomic groupings have been discerned by earlier numerical or visual studies.

## The problem of defining groups

It follows from the preceding discussion that it is absolutely essential that prior to undertaking a canonical analysis groupings of OTUs which are not unduly variable have to be defined. One method which is widely used (see chapter 2) relies upon the identification of suitable groupings from the visual study of the material and by reference to pre-existing literature. It seems that in general this approach produces reliable and satisfactory results (again see chapter 2, and especially van Vark, 1984).

The alternative, more "phenetically pure" approach relies upon the identification of morphological discontinuities by earlier phenetic studies using such statistics as Euclidean distances and PCA. This approach is particularly important when classifications are "immature", for instance when dealing with a rapidly expanding collection of fossils.

The concept of discontinuity in the identification of taxa is fundamental to phenetics. Sneath and Sokal (1973) liken the approach to the "natural method" of the French botanist Michel Adanson (1727-1806). Adanson's method aimed to discover classes which contained "no plants which do not agree together in the ensemble of their characters" (Glass, 1959). This idea was linked in Adanson's mind with the a belief in the "Great Chain of Being" and the "Principle of Continuity". Fissures in the continuity of Nature were held by Adanson to be the result of the disappearance of intermediate forms, or of ignorance of their existence. Today, knowledge of evolution allows us to add

differential rates of evolution in taxa to the list of possible causes of apparent discontinuity (see, for example, Bilsborough, 1973). It is a fundamental position of modern phenetecists that the discovery of groups is an indispensable first step in the construction of classes (Sneath and Sokal, 1973) and this approach is implicit in the work of several authors (e.g. Stringer, 1974a, Creel and Preuschoft, 1976, Brauer, 1984, van Vark, 1984).

The identification of suitable groups of fossils for Canonical Analysis

The studies of chapter 4 are principally intended to compare the results of the study of the cranial morphology of fossil groups by linear and angular measurements with those obtained by study of Fourier data. Considering the preceding discussions it is essential that the groups of fossils used in these studies are homogenous, not unduly variable and distinct.

The review of the literature presented in chapter 4 has served to illustrate that there is debate about the constitution, degree of overlap of and the number of classes represented by fossils attributed to *Australopithecus*, *Homo erectus*, archaic *Homo sapiens*, and fossil a.m. *Homo sapiens*. A further problem arises because of the need to estimate a large number of variables from the fossil material.

In order to justify the groupings submitted to the canonical analyses of chapter 4 it was necessary to undertake a series of analyses directed towards defining suitable groupings of fossil crania. In addition these studies have allowed the examination of patterns of within-group variability.

# MATERIALS AND METHODS

## A. Materials

The fossil casts used in this study are listed in table 4.1. and the modern groups used in the construction of univariate bar charts and in canonical analyses are described in chapter 2 (see table 2.1).

## B. Methods

### Measurement methods

The 34 linear and angular measurements used in this enquiry are described in chapter 2 (tables 2.2 and 2.3) and listed in chapter 4 (table 4.2). Problems of estimation of dimensions and angles are discussed in chapter 4 and in appendix A.

### Statistical analysis

#### *Univariate analysis*

It was noted in chapter 2 that the variances of variables within the modern groups were, in general, positively correlated with the magnitude of their mean values: the bigger the group mean, the bigger the variance. Following the recommendation of Sokal and Rohlf (1969: p382) the data were log transformed, this resulted in nearly equal within group variances. This equality allowed the calculation of a pooled within-group variance which was used to draw a bar chart for each of the 34 variables of table 4.2. On each bar chart the mean +/- 2 standard errors and the upper and lower 95% confidence limits of each

modern group together with the magnitude of the variable within each of the fossil specimens were indicated.

*Multivariate analysis*

Multivariate analysis comprised:

a) The calculation of a matrix of Euclidean distances between fossil material using data which were scaled, by ratio, for the square root of the area of the midline projection of each cranium.

b) Two series of principal component analyses of correlation matrices of the data from the fossil crania.

*I. Analyses of 34 raw variables*

The 34 variables listed in table 4.2 were submitted to principal component analyses using the S.A.S. (1982) package. Groups were identified by discontinuities in the pattern of overall variation as represented by the scores of individuals on principal components. The patterns of variation within these phenetic groups were then assessed by further principal components analyses. The influence of size on the observed patterns of variation was examined by calculating the correlation of the scores of individuals on each component with their "size" (the square root of the midline area).

*II. Analyses of 34 scaled variables*

It was clear from the results of the studies described above that size had a considerable effect upon the observed patterns of variation between the fossil crania. For this reason an identical series of principal component analyses was undertaken using data adjusted (by ratio) for differences in the midline areas of each cranium. The calculation of the correlation of the scores of individuals on principal components with their sizes allowed the investigation of patterns of size related shape change (see ch. 3).

It can be argued that the use of correlation matrices may give rise to distortions in the resultant PCAs because equal weighting is given to characters irrespective of their magnitude. The converse argument can be applied to analyses based upon variance–covariance matrices, that undue weighting is given to character magnitude. The choice of correlation matrices was made after preliminary analyses using both correlation and variance–covariance matrices resulted in virtually identical results.

c) The PCAs outlined above failed to clearly define the affinities of certain crania (Skhul V and Steinheim, see results, later) and conflicted with the results of other workers in their attribution of the Kabwe 1 cranium so two canonical analyses designed to clarify the fossil groupings were undertaken. These employed

34 scaled variables (table 4.2) from the fossil crania and from the crania of the negro and chimpanzee groups described in chapter 2 (table 2.1). In the first canonical analysis the problematic crania were included in the group to which they appeared most similar and in the second they were excluded.

# RESULTS

## A. Univariate analysis

The univariate bar charts produced using log transformed data and pooled standard deviations are presented in appendix C.

The results of the univariate studies are best considered in two parts; first the patterns of difference which are demonstrated between the modern crania and second those patterns which exist between the fossil crania.

Study of the bar charts shows a clear split between the humans and the apes in a large number of dimensions. In general the dimensions from the human populations are larger than those from the apes, the exceptions are upper facial height, palatal length, basi–prosthion length and basi–staphylion length. This pattern of differences reflects the fact that the ape neurocrania are generally smaller than human ones but ape faces are more prognathous.

There are some variables in which the separation between apes and men is less marked. These include foramen magnum length, the angle lambda–opisthion–basion, palatal breadth, nasal breadth, subnasal height, orbital height and breadth, infraorbital breadth and the angle nasion–basion–prosthion.

The positions of the fossils on the charts are less easy to summarise. In general there are two groups of fossils: those which consistently share very similar values of most variables with the human populations and those which show a more variable pattern of similarities. In the first group can be placed all

of the fossils of recent *Homo sapiens*, the Steinheim cranium, Skhul V, Kabwe, and all of the "classic" Neanderthal crania. The second group includes all the remaining crania and shows much more variability.

In general the *erectus* grade casts are more similar to the humans than the apes. They show a large within-group variability in some dimensions: in palatal length and breadth Weidenreich's reconstruction of a female Sinanthropus is very large, far larger than any modern human and the within-group variability in these dimensions is larger than that seen in any extant species.

A problematical group of fossils comprises early *Homo* and the australopithecines. No clear pattern of relationships can be seen. In some variables they are similar and ape-like (occipital chord, cranial breadth and postorbital breadth); in others they are similar and human like (parietal height, parietal chord, basi-prosthion length and angle nasion-bregma-lambda) in the remainder they show a mixture of ape-like and human-like features. No obvious groupings emerge.

## B. Multivariate analyses

### I. Principal Components Analyses

### Raw data

The plots of the scores of fossils on the lower order principal components are given in figures B.1 to B.9. Figure B.1 illustrates the results of an analysis in which all fossils were submitted to PCA. The abbreviated fossil names which are used in all plots of PCAs are generally self evident, they are also given in table 4.1 for clarity. Figures B.2 to B.9 illustrate principal component analyses which were carried out upon the phenetic groupings discernable from the studies of figure B.1. These further studies concentrate on the examination of patterns of variation between individuals which scored low, intermediate, and high values on PCI, of figure B.1. These three groups comprised material which has been attributed to *Australopithecus* and *Homo habilis*, to *Homo erectus* and to fossil subspecies of *Homo sapiens*. The proportion of the total variance which is accounted for by the first five principal components from each study is given in table B.1a. The correlations of the scores of individuals on these first five PCs with the size variable (square root of the midline area) are given in table B.1b.

#### *a. PCA of all fossil crania*

In figure B.1 are presented plots of the first four principal components from the analysis of all the fossil crania. It can be seen from table B.1a that these four PCs between them express 73% of the total within group variance and from table B.1b that the first component is the only one which shows a

FIGURE B.1 – Principal Components Analysis of 34 raw linear and angular dimensions

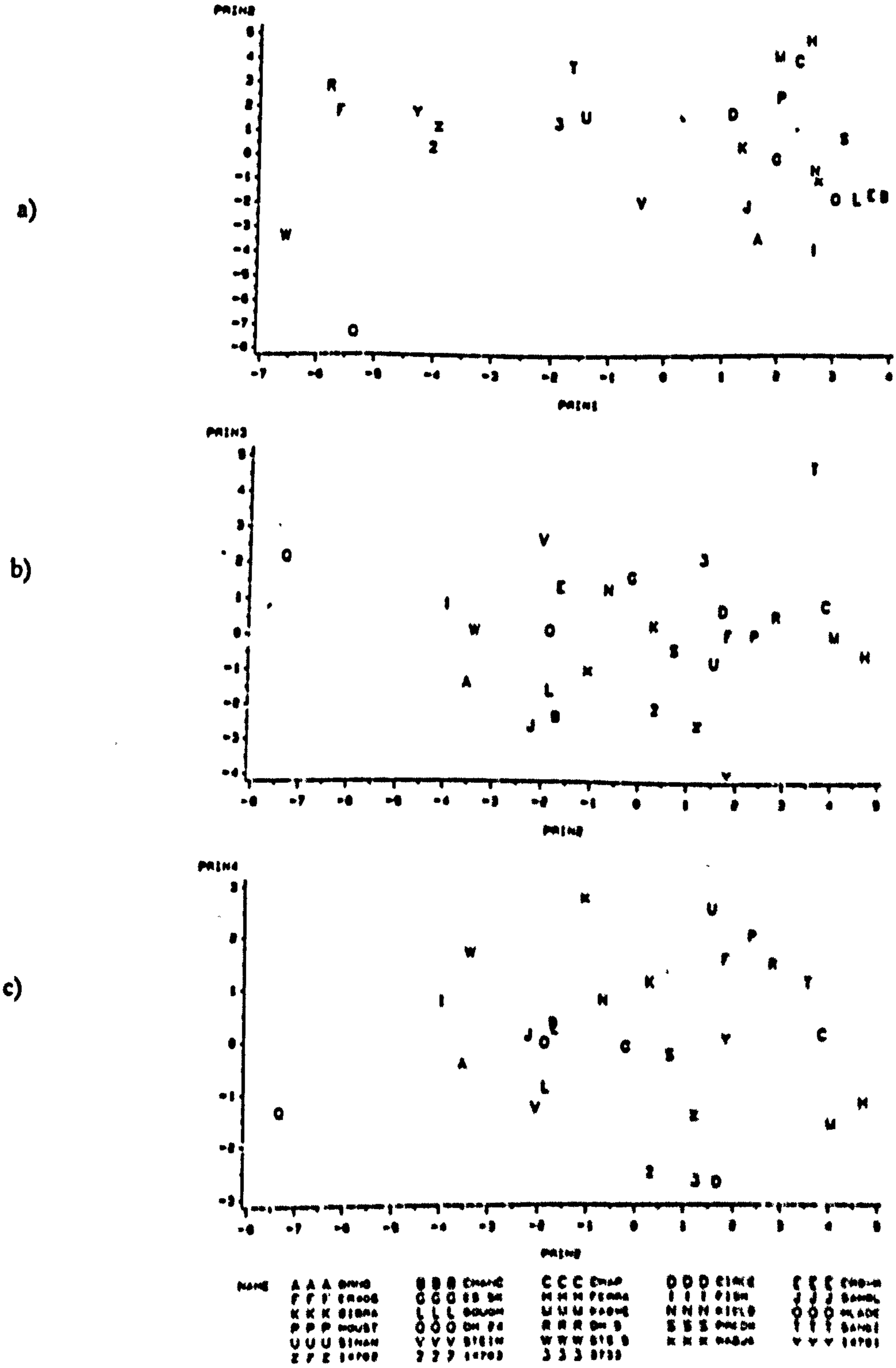



Fig B.1

## TABLE B1

### Principal component analyses of 34 raw variables

a. The cumulative proportions of the total variance expressed on each PC(%)

| PC | I | II | III | IV | V |
|---|---|---|---|---|---|
| GROUP | | | | | |
| All Fossils | 34 | 57 | 67 | 73 | 80 |
| *H. Sap.* subsp. | 34 | 50 | 62 | 72 | 80 |
| a.m. *H. sap.* | 29 | 49 | 66 | 76 | 85 |
| Neanderthals + archaic *H.sap* | 40 | 59 | 74 | 84 | 92 |
| Apiths + *H. hab.* | 46 | 70 | 87 | 96 | 99 |

b. The correlation of the size variable with individual scores on PCs I – V

| PC | I | II | III | IV | V |
|---|---|---|---|---|---|
| GROUP | | | | | |
| All Fossils | 0.96** | 0.20 | −0.06 | 0.00 | −0.11 |
| *H. Sap.* subsp. | 0.21 | 0.84** | 0.33 | −0.22 | −0.12 |
| a.m. *H. sap.* | 0.74** | −0.29 | 0.32 | 0.29 | −0.12 |
| Neanderthals + archaic *H.sap* | 0.94** | 0.20 | −0.18 | 0.04 | 0.04 |
| Apiths + *H. hab.* | 0.97** | 0.10 | −0.04 | 0.17 | 0.07 |

P < 0.01 = **
Others are NS

strong correlation with cranial size ($r = 0.96$, $P < 0.001$).

Figure B.1a is a plot of PCI vs. PCII from this analysis. Several clumpings of crania are clearly seen. The largest group comprises all the "classic" Neanderthals, recent fossils of *Homo sapiens*, the Kabwe cranium, Skhul V and, peripherally, the Steinheim cranium.

A group of crania which have been attributed to the grade of *Homo erectus* form a central cluster, these are KNM–ER 3733, Weidenreich's reconstruction of "*Sinanthropus*" and his reconstruction of the Sangiran 4 cranium. The pattern of within–group variability of these "*erectus*" grade crania which is demonstrated in this study should be regarded with caution: all three crania have been heavily reconstructed and the Asian representatives are almost entirely sculpted.

A third cluster is formed by the three reconstructions of KNM–ER 1470 and a fourth clear grouping is that of OH 5 with KNM–ER 406, these two crania lie close to each other even on PCs III and IV (figs B.1b and c).

Two fossils which are outliers are Sts 5 and OH 24. They do not form a tight cluster though Sts 5 is the nearest cranium to OH 24 on the combination of PCs I and II.

It has already been noted that the scores of crania on PCI correlate highly with the square root of their midline areas (note this may not be a simple size relationship – see Ch. 3). PCII seems to reflect a different phenomenon which might be described as "robusticity". Crania which score highly on PC II are the Neanderthals, Sangiran 4 and OH 5 and KNM–ER 406. Low scores on PC II characterise the less robust crania such as OH 24, Sts 5 and fossil a.m. *Homo*

No clear significance can be attached to the scores of fossils on PCs III and IV.

The remainder of the principal component analyses using 34 raw cranial dimensions were directed to the examination of patterns of variation within the phenetic groups identified in this first PCA. The three main groupings are the subspecies, archaic and anatomically modern of *Homo sapiens*, the grade of *Homo erectus*, and the australopithecines and early *Homo*.

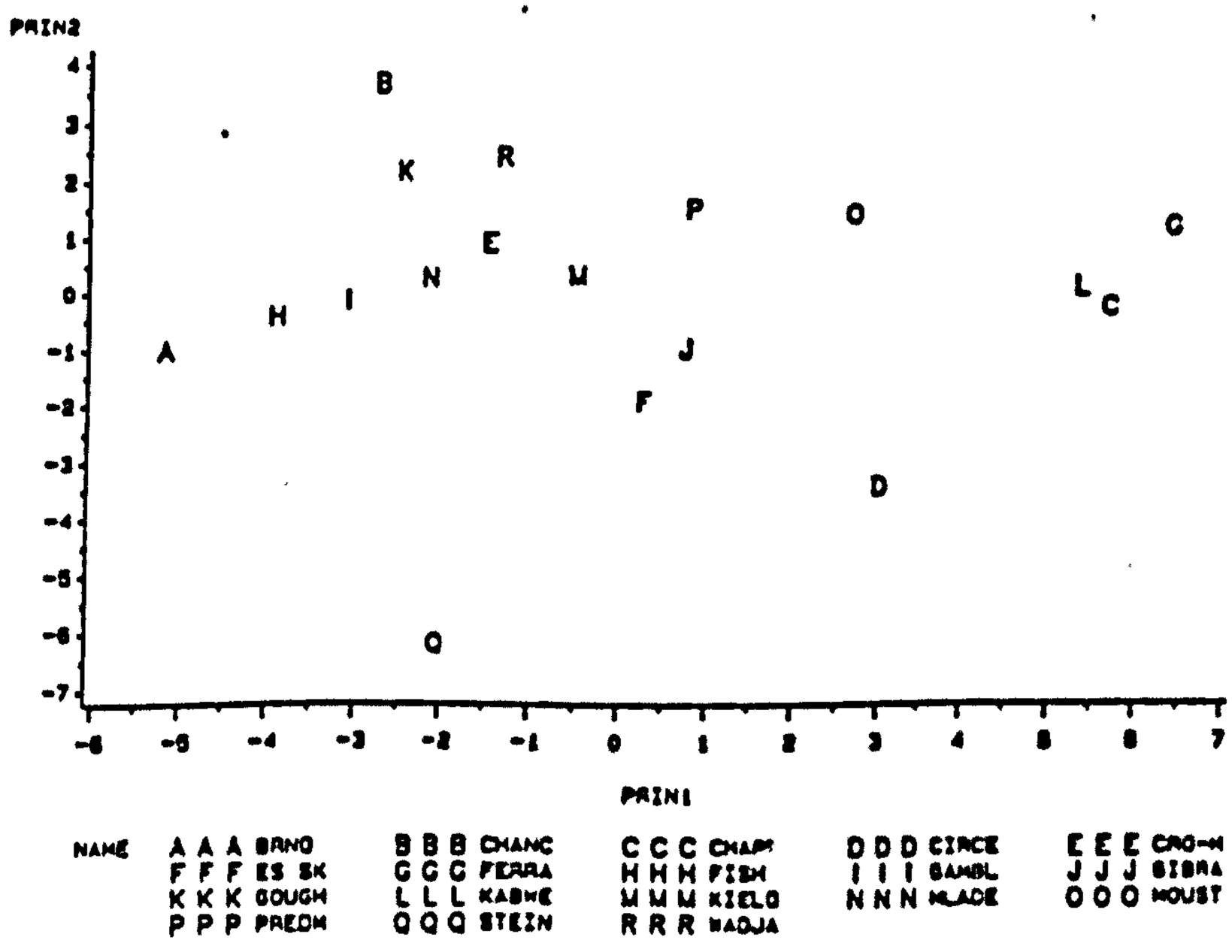
*b. Archaic and fossil a.m. Homo sapiens*

Figure B.2a is a plot of PCI vs. PCII from the analysis of these crania. The major part of the variance within this collection of crania is expressed along PCI, this PC correlates only 0.21 (N.S.) with cranial size (table B.1b). Large scores on PCI are obtained by robust crania, small scores by more gracile ones. The split between Neanderthal and Neanderthal-like crania and more modern ones occurs at about the middle of PCI but it is by no means clear cut. The crania from Predmost, Gibraltar and es-Skhul all have very similar locations though, in general, the more recent crania have a lower score.

Scores on PCII correlate very well with the size variable (table B.1b, $r = 0.84$, $P < 0.001$). and the clearest distinction to be observed on it is the separation of the Steinheim cranium from all the others. The average value for the square root of the midline area in the "classic" Neanderthals and Neanderthal-like crania is 15.03cm, that for Steinheim is 13.57cm. Principal component III (fig

FIGURE B.2 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




b)

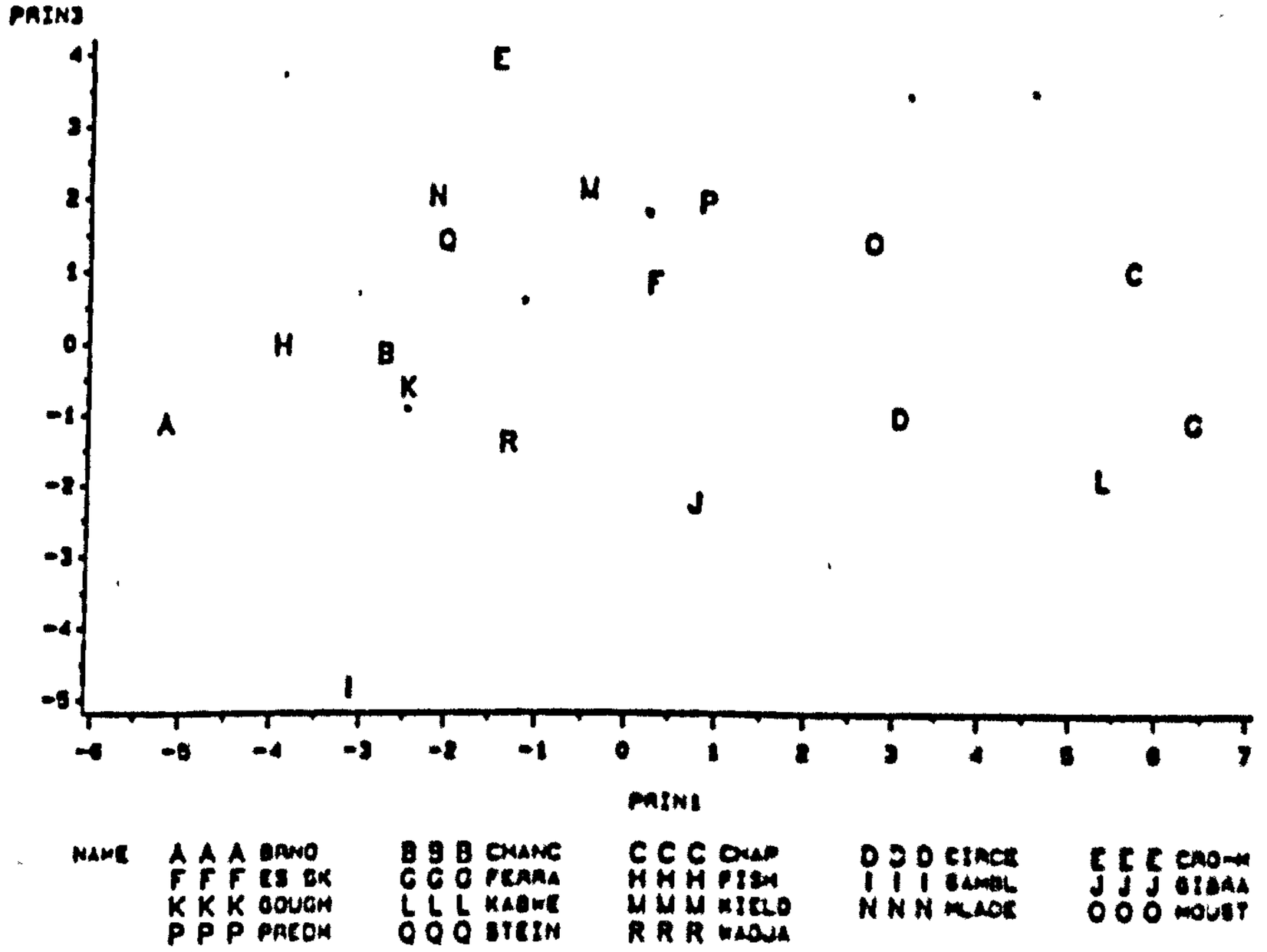



Fig B.2

B.2b) contributes little to the problem of group identification.

In Figure B.3a is presented a three dimensional plot of PCs I vs II vs III. Pyramids symbolise the Neanderthal and Neanderthal–like crania and Steinheim, circles indicate the more modern crania. It is clear from this diagram that no clear distinction between the Neanderthal and Neanderthal–like and more modern crania can be made on the basis of the first three components. From figure B.3b it can be seen that PCIV also fails to help in this matter.

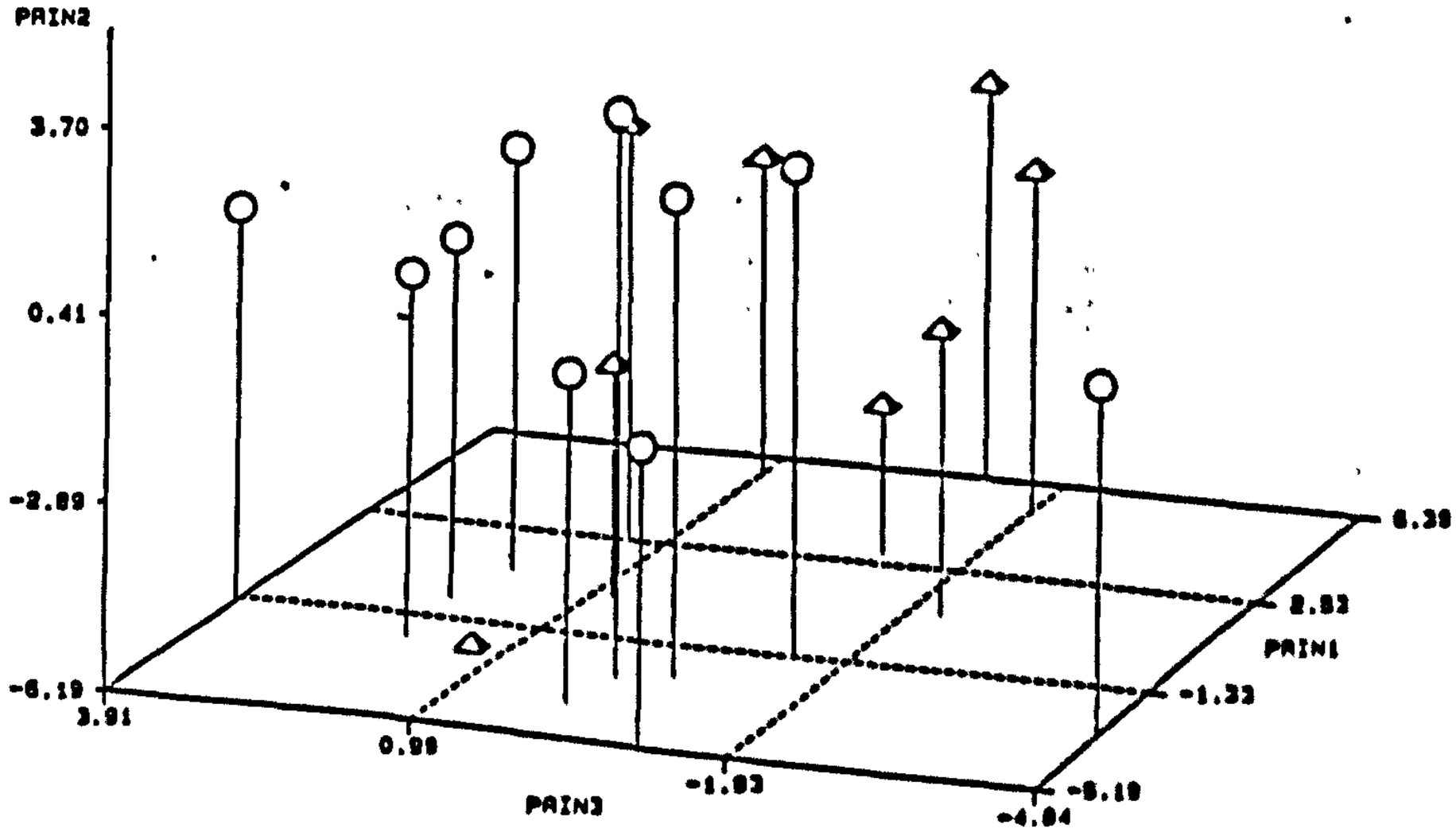
The fact that Neanderthal and Neanderthal–like crania are not distinguished clearly from more modern ones is at first sight alarming since these crania can be readily distinguished by eye. The problem, however, is less severe than appears at first sight. Later studies will demonstrate that the effects of size come to so dominate the phenetic relationships between crania that a degree of confusion occurs. For now the reader will be asked to accept that the Neanderthal and Neanderthal–like crania are phenetically distinguishable from the more modern human crania. On this basis two further principal component analyses were carried out: one on the recent fossils of *Homo sapiens* and one on all of the Neanderthal and Neanderthal–like crania plus the Steinheim cranium.

*c. Recent fossils of Homo sapiens.*

Figures B.4 and B.5 are plots from the principal components analysis of the recent fossils of *Homo sapiens*. These fossils have been recovered from a wide geographical area. They are of unclear sexual attribution.

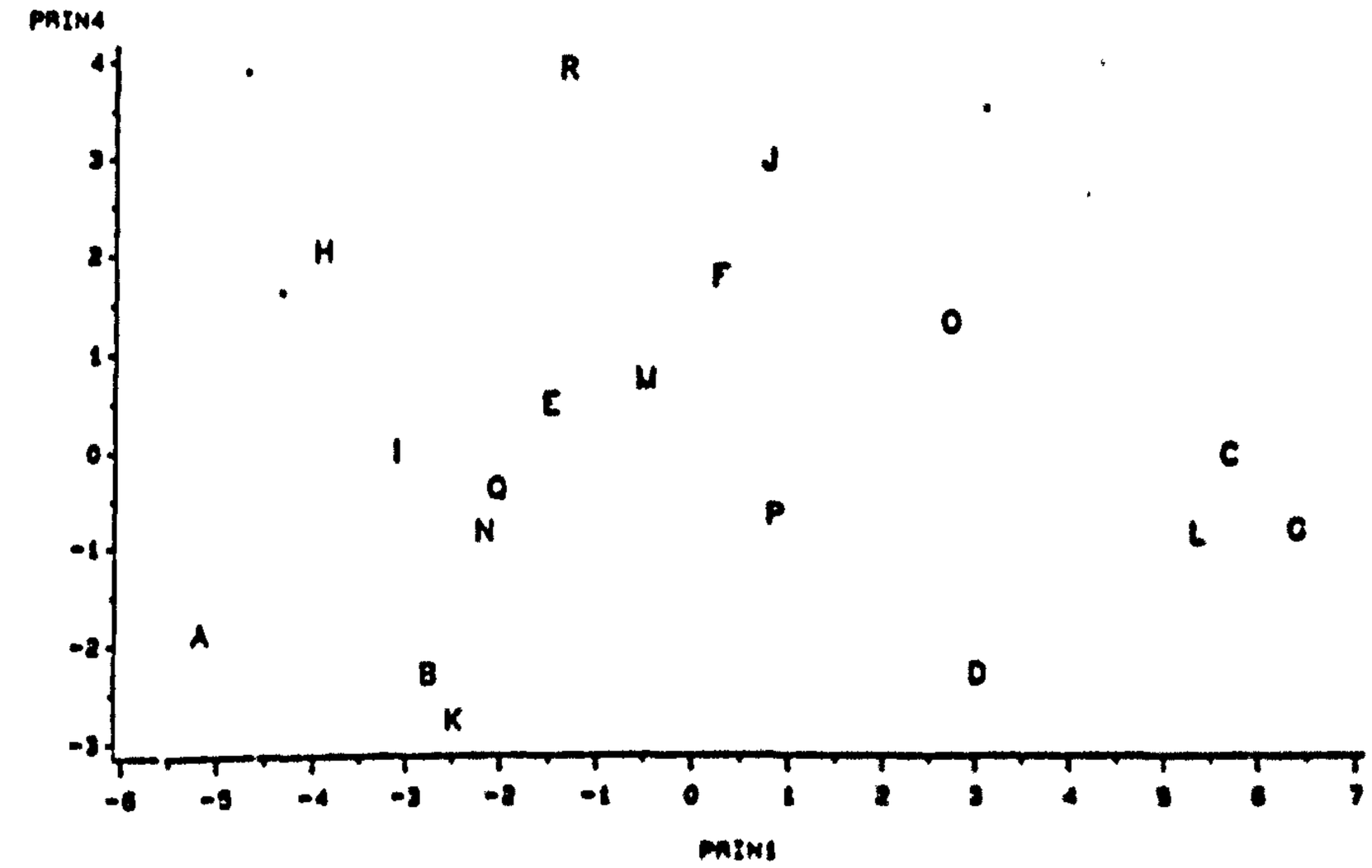
FIGURE B.3 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




Key:– Pyramids = Neanderthals + Neanderthal – like crania
circles = am crania

b)

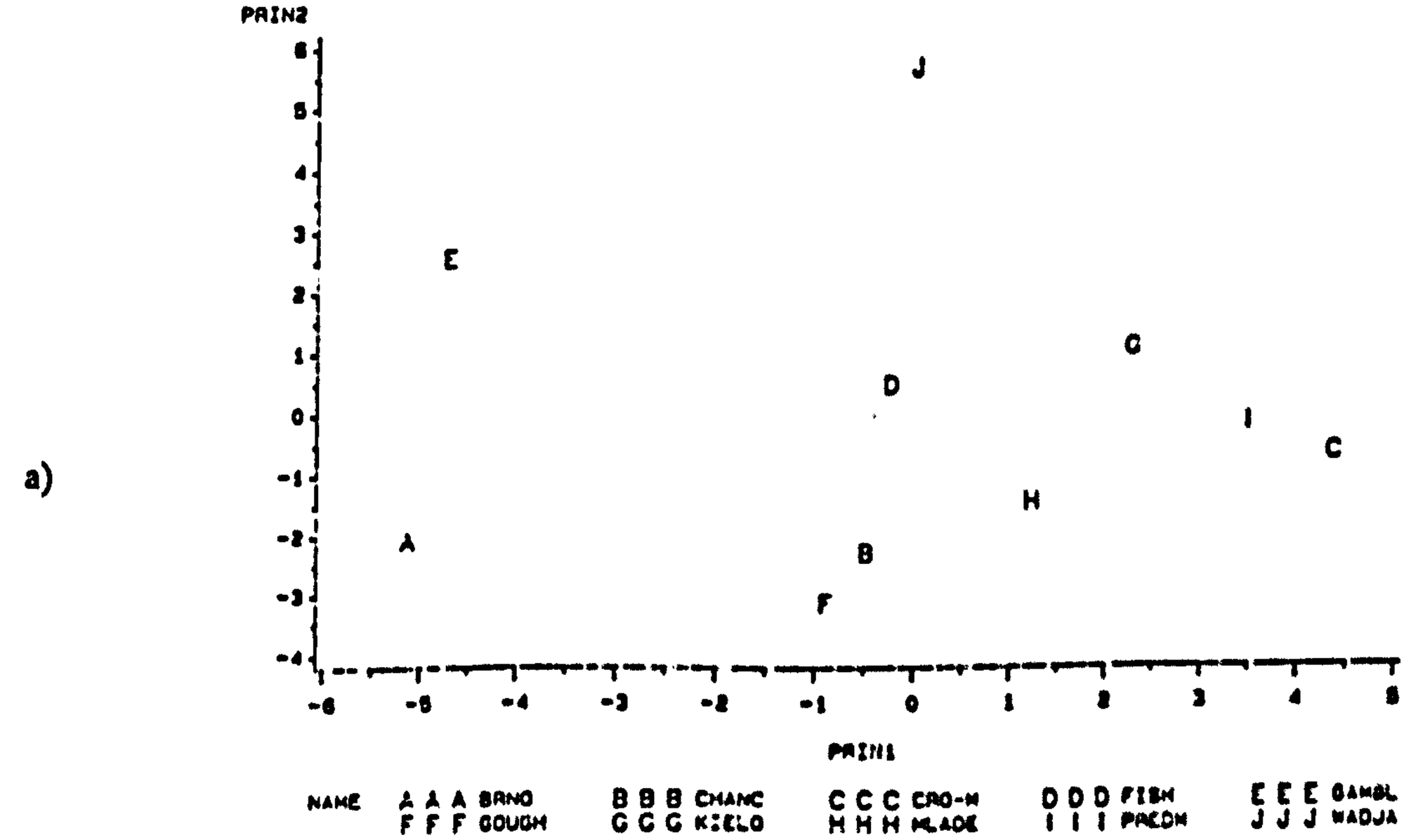



| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NAME | A | A | A | DMNO | B | B | B | CHANC | C | C | C | CHAP | D | D | D | CIRCE | E | E | E | CRO-M |
| | F | F | F | ES BK | G | G | G | FERRA | H | H | H | FISH | I | I | I | GAMBL | J | J | J | SIBRA |
| | K | K | K | GOUGH | L | L | L | KABWE | M | M | M | KIELO | N | N | N | MLADE | O | O | O | HOUST |
| | P | P | P | PREDM | Q | Q | Q | STEIN | R | R | R | WADJA | | | | | | | | |

Fig B.3

FIGURES B.4 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




b)

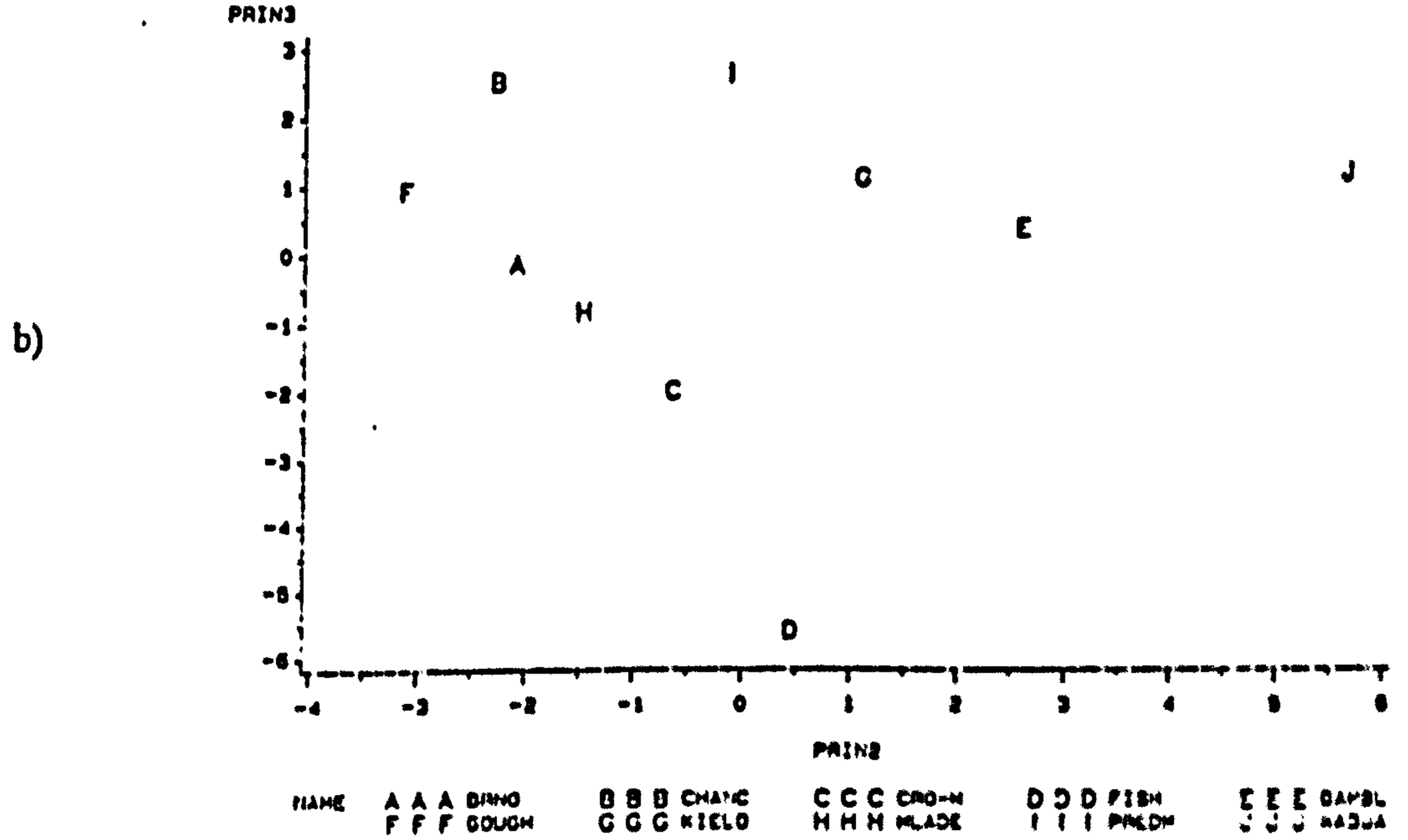
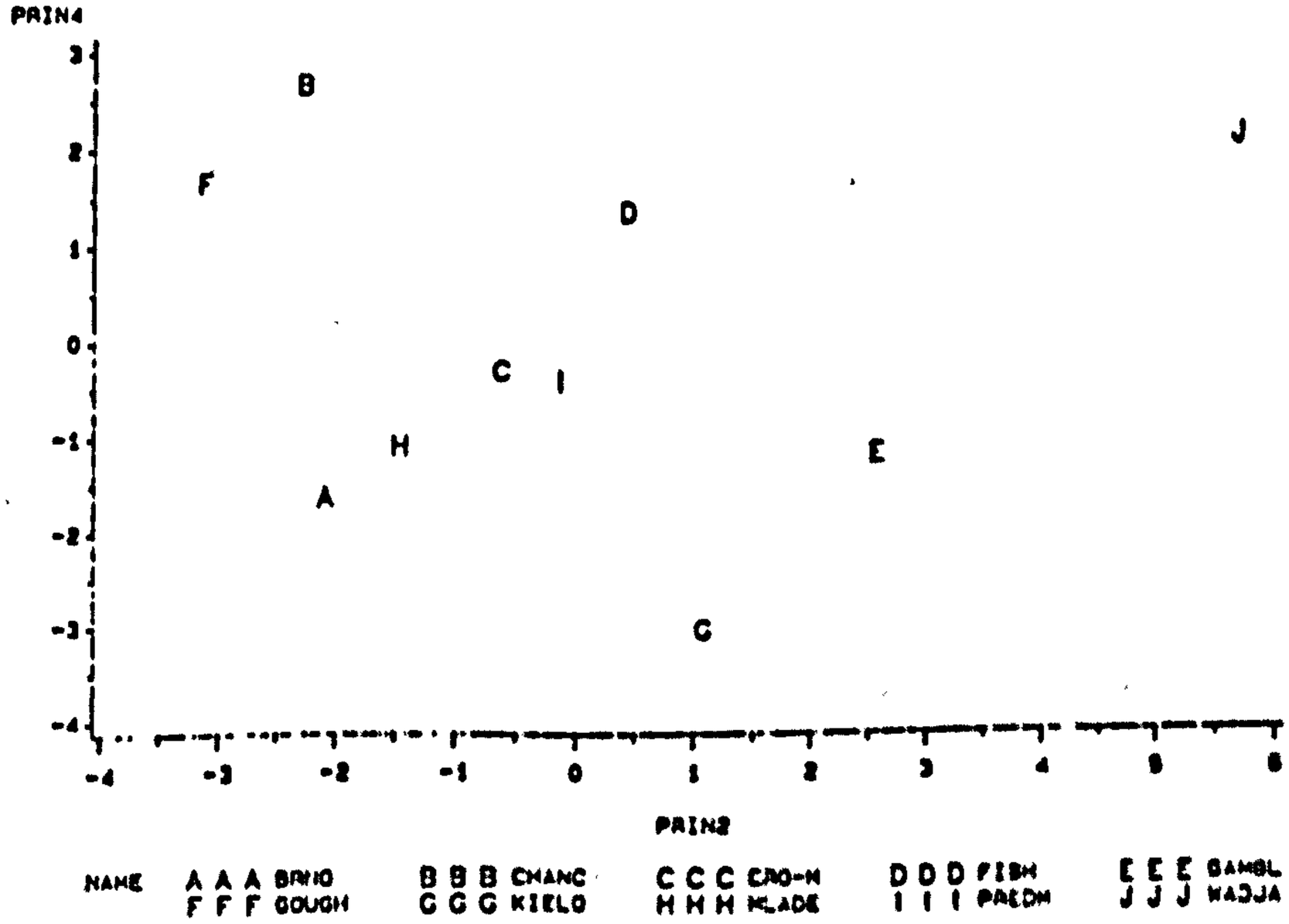



Fig B.4

FIGURE B5 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




b)

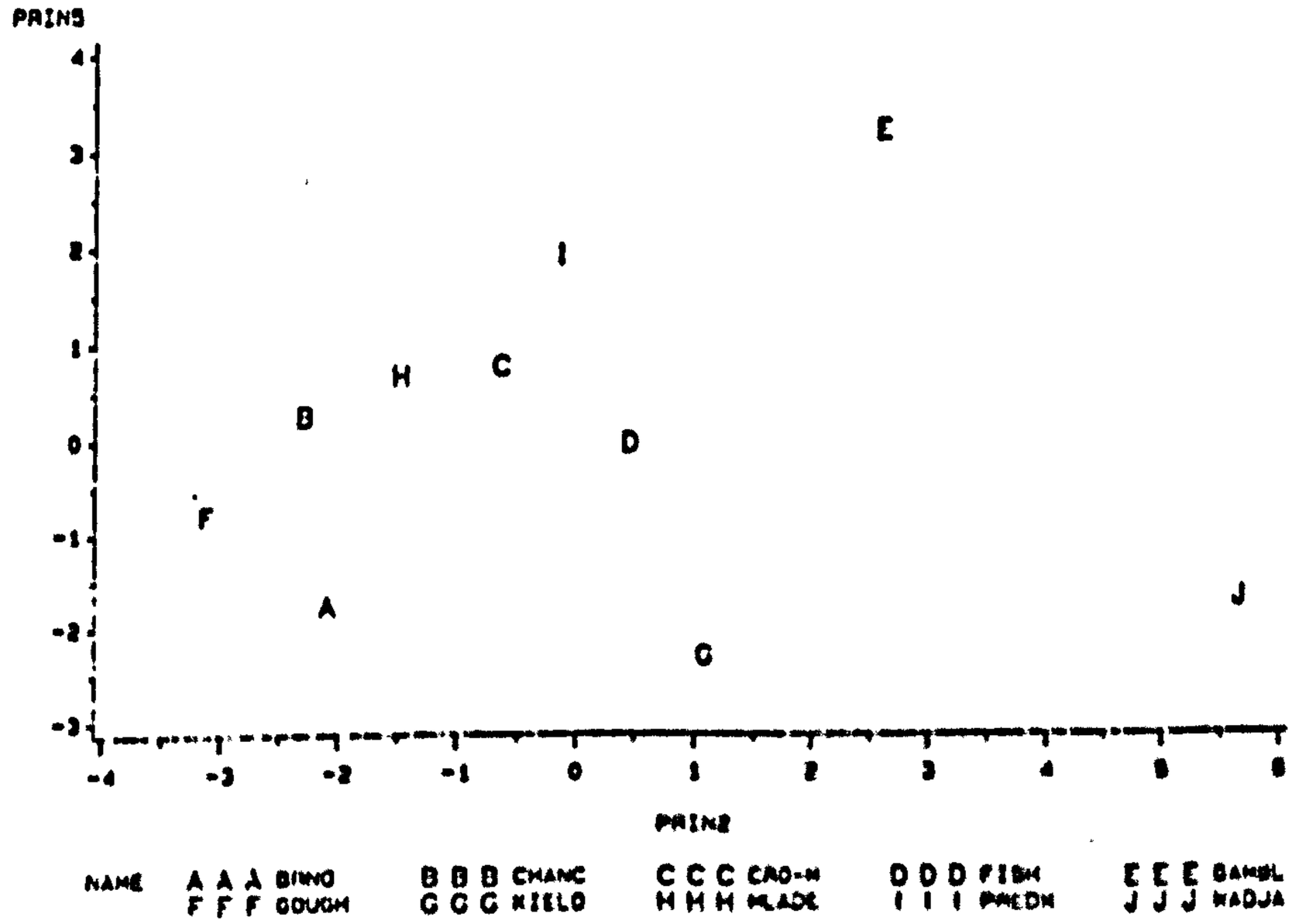



Fig B5

The plot of PCI vs PCII accounts for only 49% (table B.1a) of the total within group variability, higher PCs need to be examined in order to obtain a fuller picture. There are, however, several interesting points which arise from the study of individual PCs. PCI correlates 0.74 ($P<0.001$) with the size variable (table B.1b) the smaller crania have negative scores, the larger, positive.

PCs II, III, IV and V seem to reflect geographical differences. On PCII negative scores characterise the European crania and positive scores the fossils from further afield. Thus, the fossil from Java, Wadjak 1 has the largest score on PCII, next is the fossil from East Africa, Gamble's cave 1 this is followed by the Keilor 1 and the Fish Hoek 1 crania. These last two are not markedly separated from the European material. Their distinctive features are more clearly emphasised by higher components. The Fish Hoek 1 cranium is clearly separated from all the others by PC III and the Keilor 1 cranium is well separated by PCs IV and V. PCV has, at its other extreme the Gamble's cave 1 cranium.

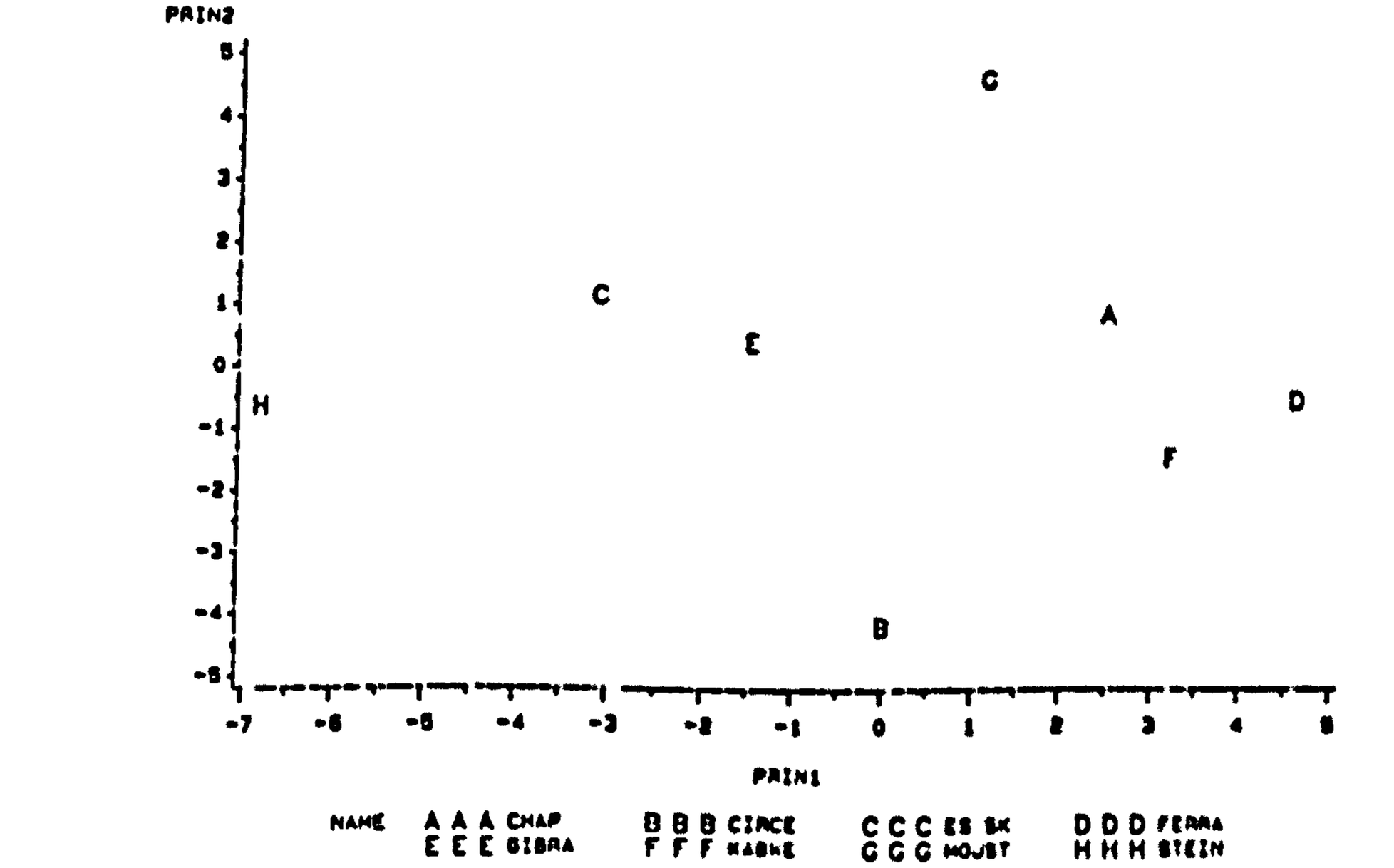
The overwhelming picture of these PCAs is one of an homogenous group of European fossils and a more disparate collection of African and Australasian fossils. Each of the fossils from outside Europe differs from each of the others in a different way.

*d. Neanderthals, Kabwe 1, Skhul V and the Steinheim cranium.*

The plots which resulted from the PCA of these crania are given in figures B.6 and B.7. PCI correlates well with size (table B.1b – $r=0.94$, $P<0.001$) and

FIGURE B.6 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




b)

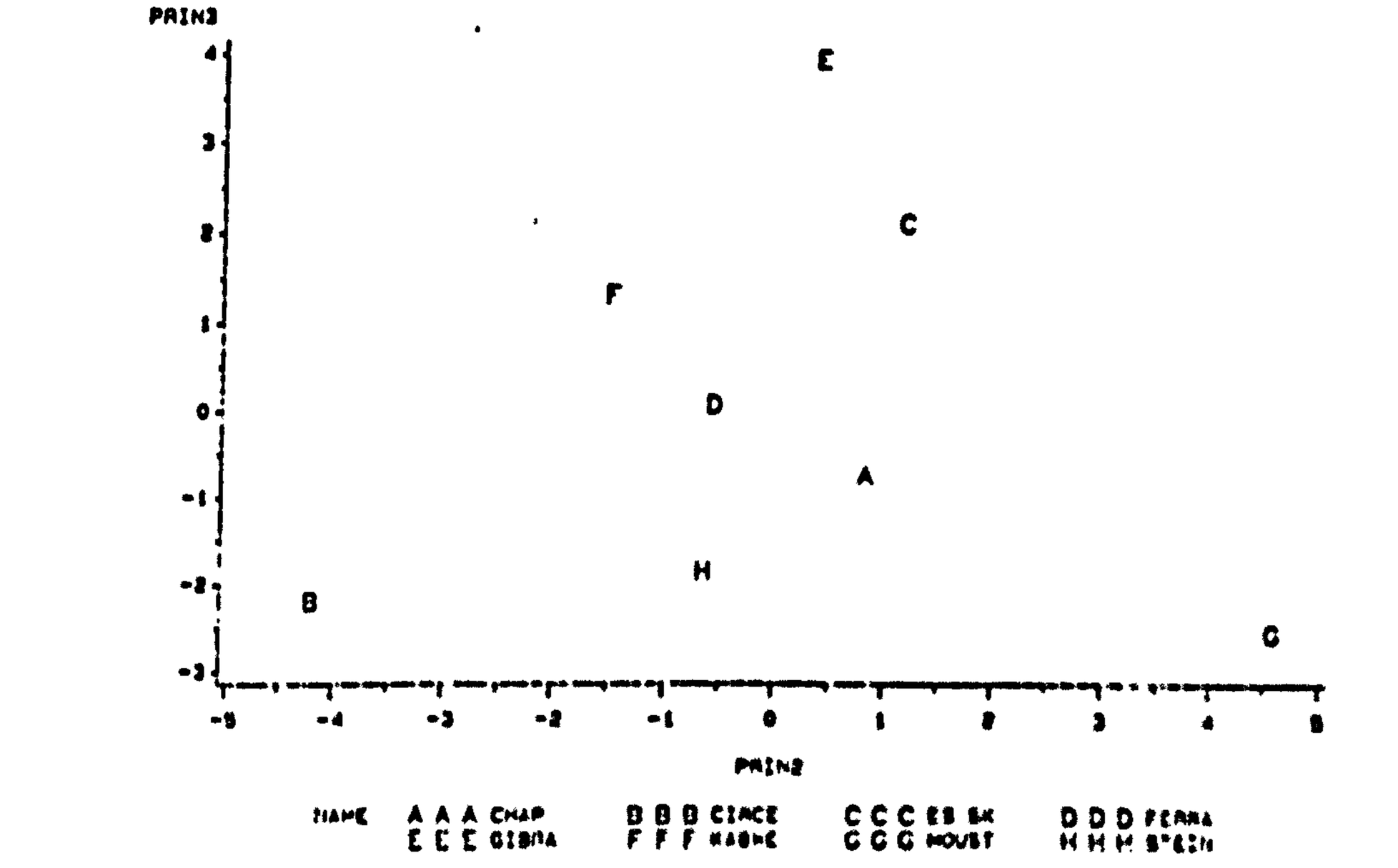
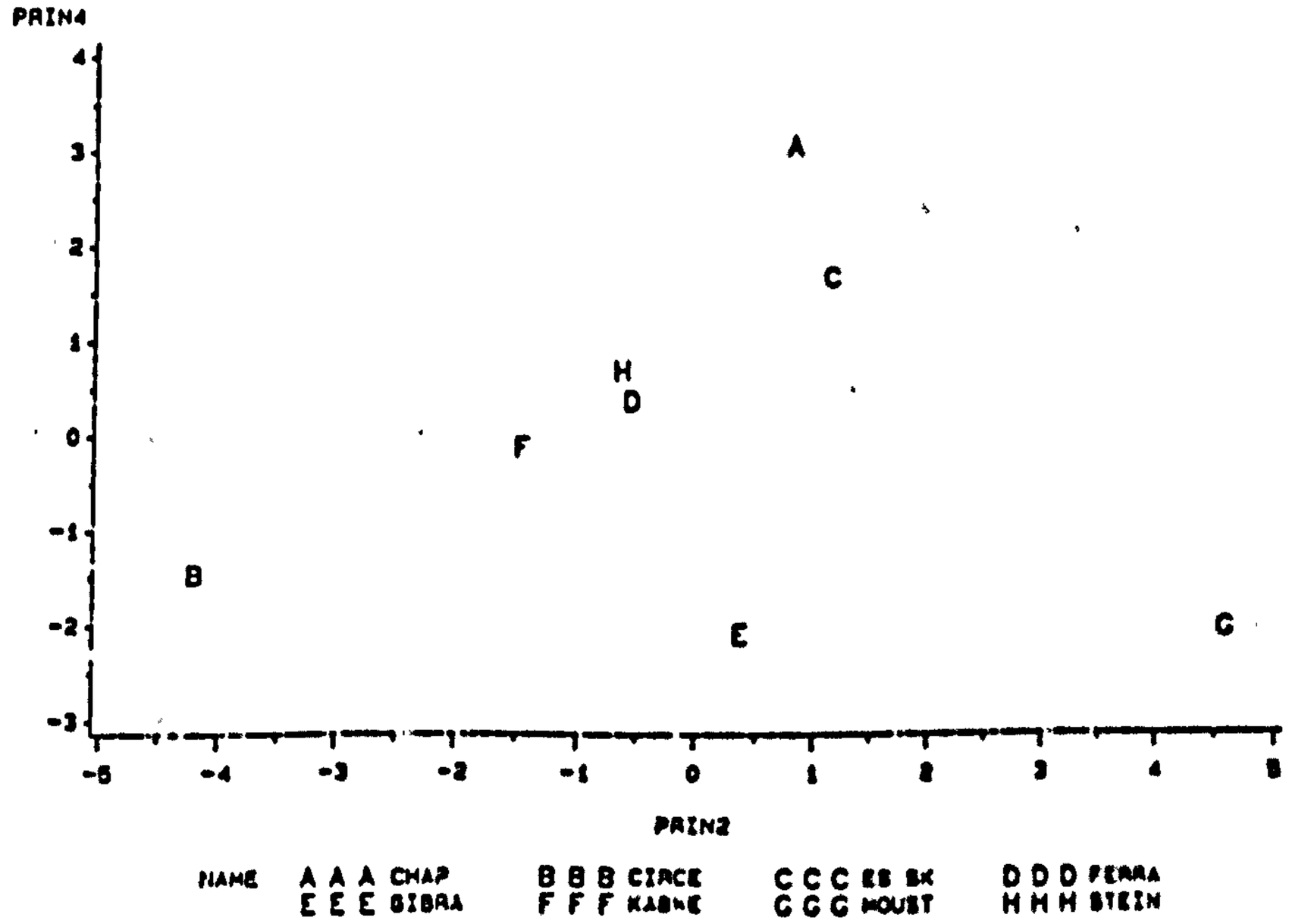



Fig B.6

FIGURE B.7 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




b)

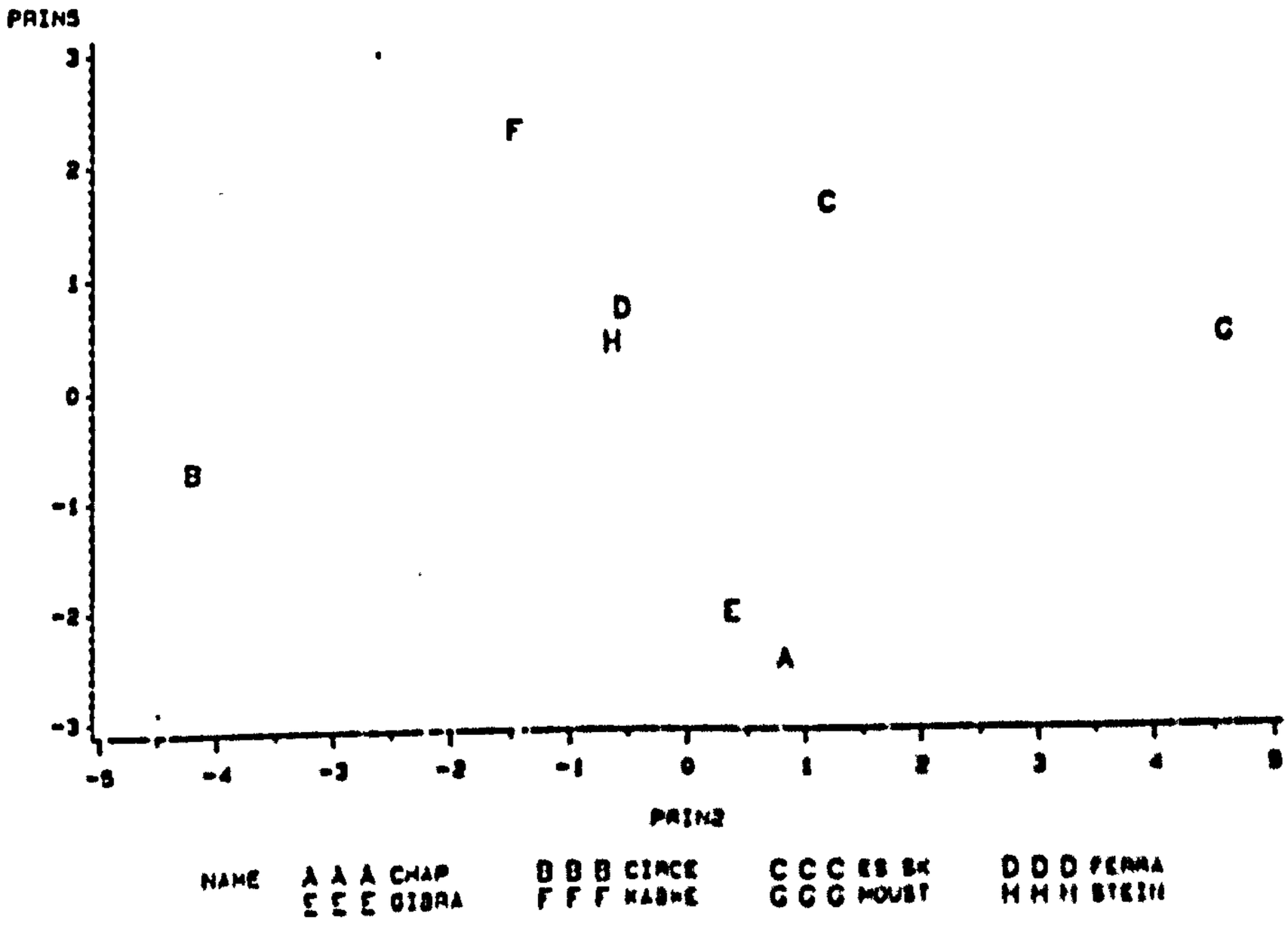



Fig B.7

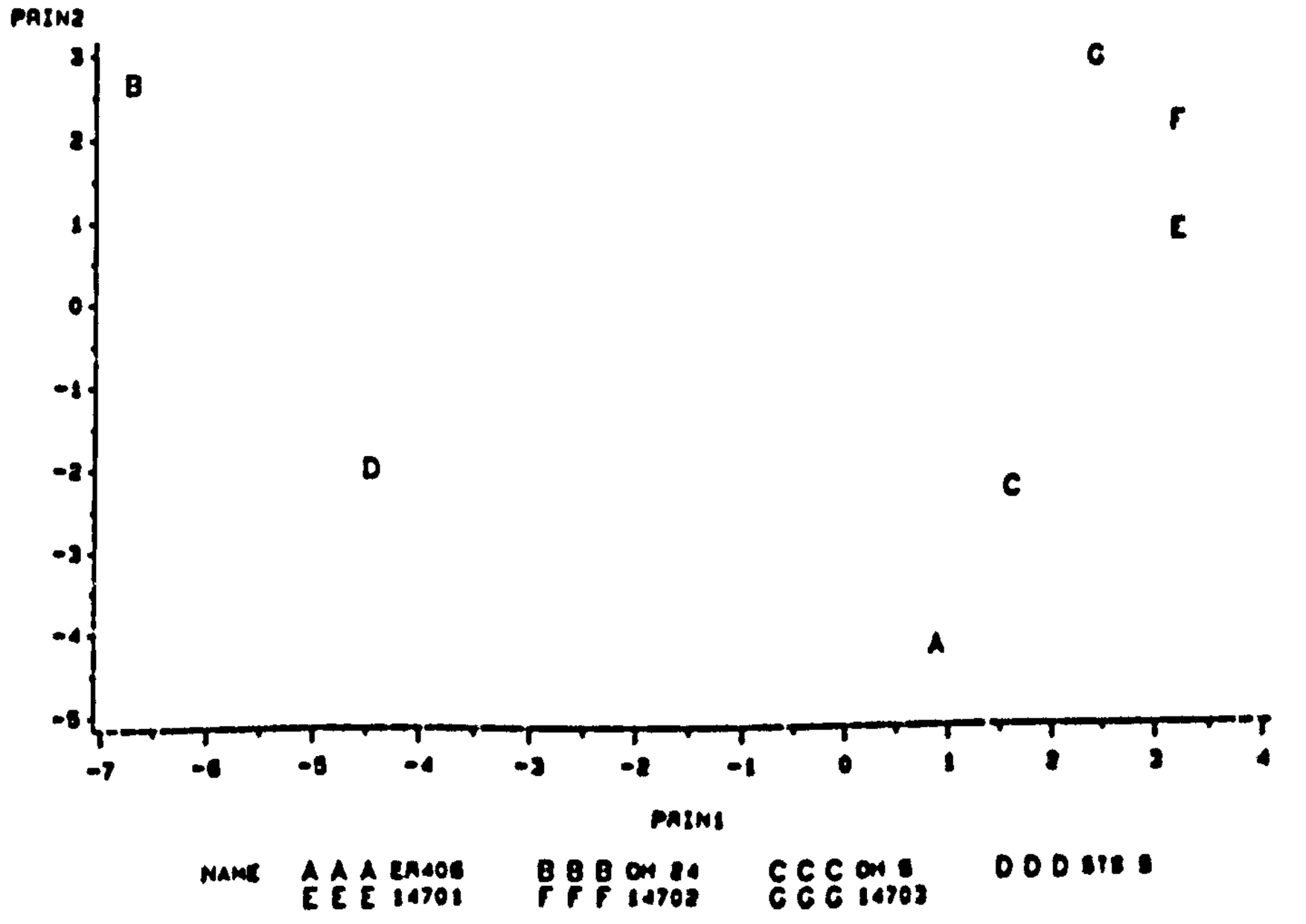
this accounts for 40% (table B.1a) of the total variability. The Steinheim cranium is the smallest of this group and occupies the most negative score on PCI. Next is placed the Skhul V cranium. The other extreme of PCI is occupied by La Ferrassie 1. A clear point which arose from the studies of chapter 3 was that care must be taken in interpreting the first PC as a pure size vector despite a high correlation with the size variable. This is because there may be an underlying size/shape relationship. Further light will be cast upon this point by the studies using scaled data.

PC II has the cranium from Le Moustier at its positive extreme and that from Monte Circeo at the negative extreme. The Le Moustier cranium is separated by about 3 SDU from the remainder of the crania and the Monte Circeo cranium by about 2 SDU. The cranium from Le Moustier is believed to be that of an adolescent, the shape change described by this PC is orthogonal to that on the "size" component, PCI. It is possible, therefore, that the Le Moustier cranium differs from the remainder in a way which is not purely related to the static allometry observed amongst adults, but to a pattern of growth allometry which is different, it should be noted, however, that the specimen is poorly reconstructed. The reasons for the nearly equal but opposite distinction afforded to the Monte Circeo cranium are less clear, perhaps growth plays a part in this too, however it seems that the cast available in the British Museum is largely sculpted (Stringer, pers. comm.) and as such is not an accurate representation of the original shape.

On the higher PCs (fig. B.6 and B.7) some of the other crania are distinguished. PCIII distinguishes the Gibraltar 1 cranium, PCIV the cranium

FIGURE B.8 – Principal Components Analysis of 34 raw linear and angular dimensions

a)




b)

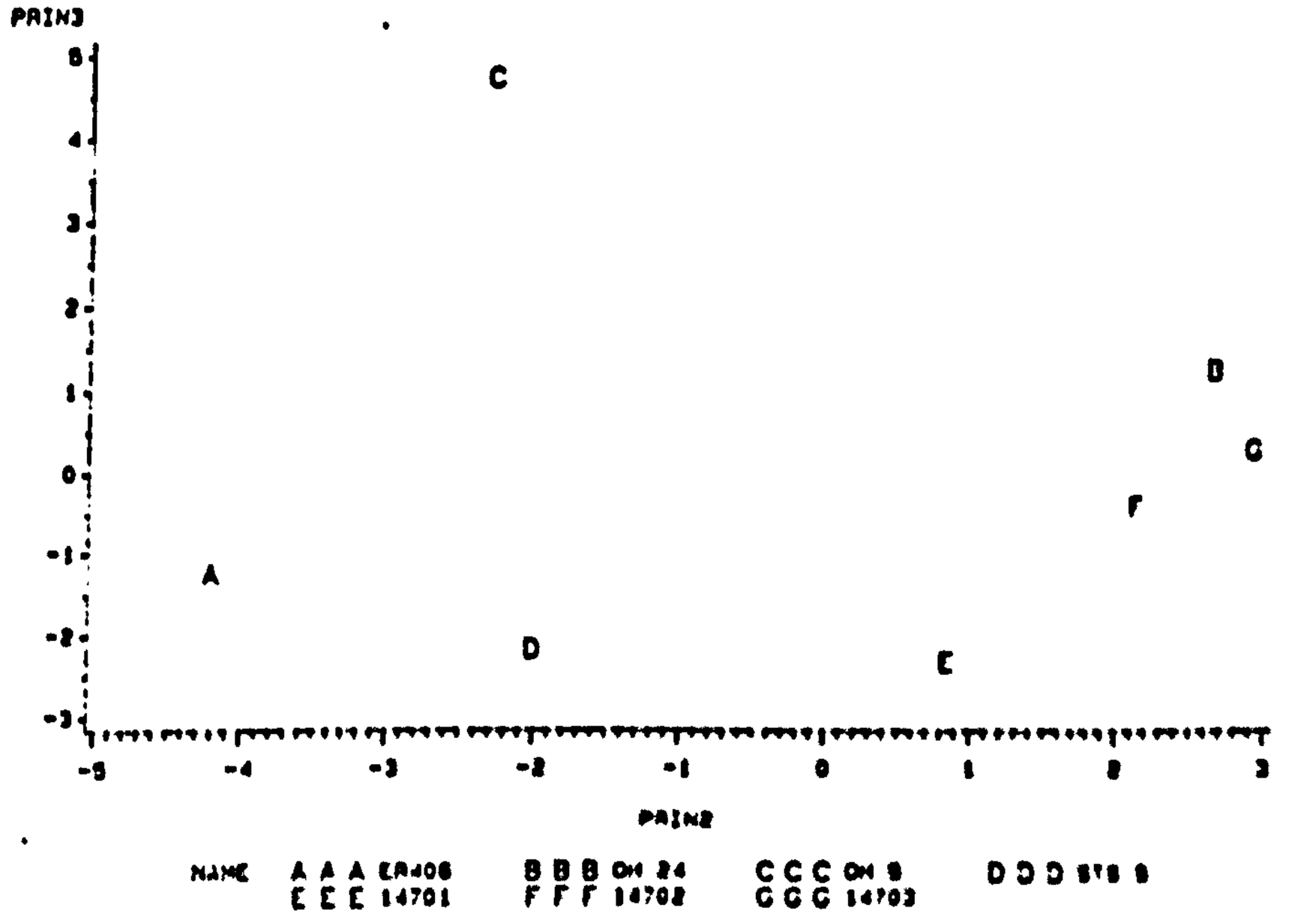



Fig B.8

FIGURE B.9 – Principal Components Analysis of 34 raw linear and angular dimensions

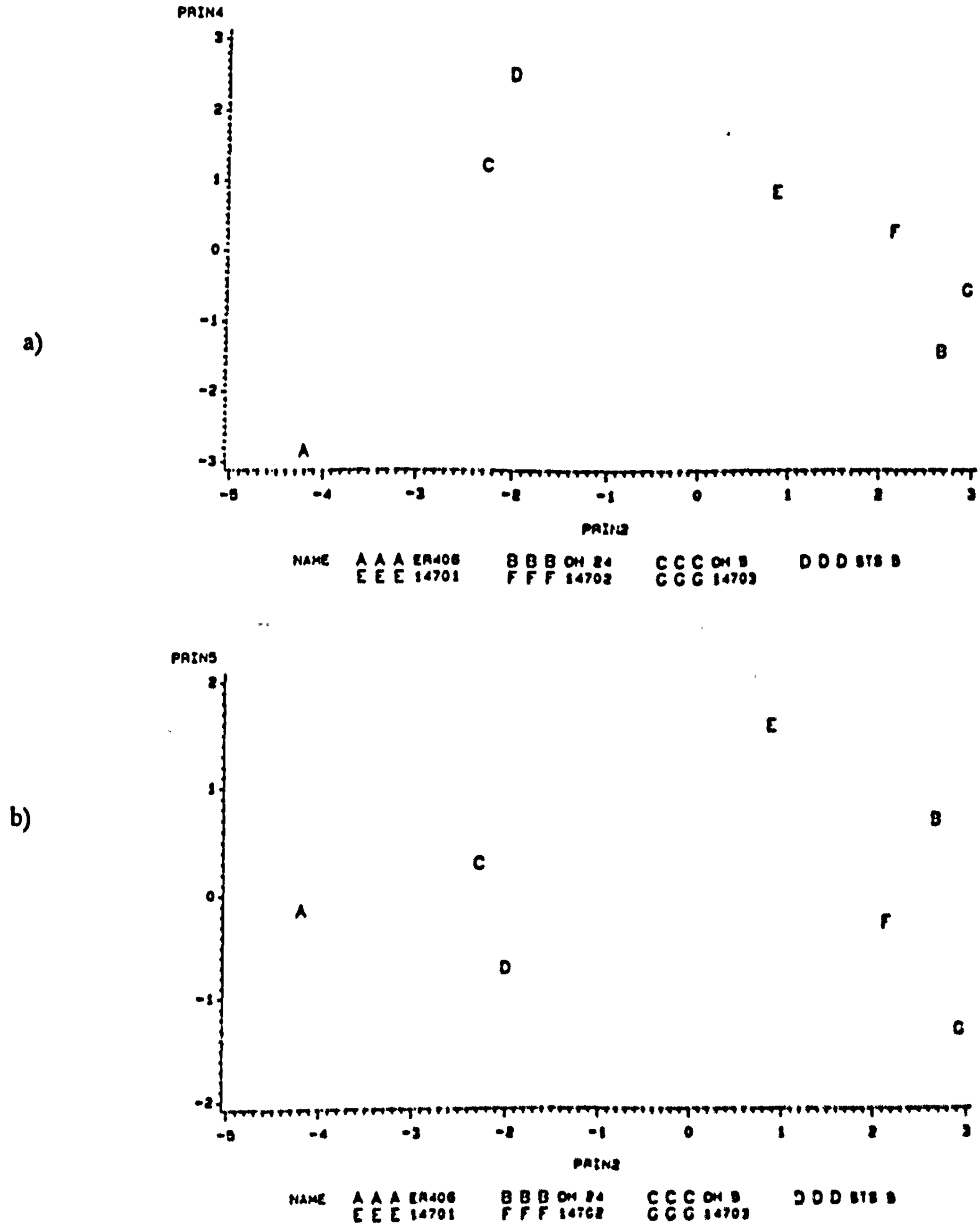



Fig B.9

from La Chapelle-aux-Saints, and PCV the cranium from Kabwe.

*e. Australopithecines and early Homo*

The PCA of this grouping produced the plots presented in figures B.8 and B.9. PCI correlates strongly with the size variable (table B.1b – $r=0.97$, $P<0.001$), accordingly KNM-ER 406, OH 5 and the three reconstructions of KNM-ER 1470 occupy the positive pole and Sts 5 and OH 24 the negative one. Again, in the light of the studies of ch. 3 care must be taken in interpreting this as a pure size component.

The spread of crania along PCII is interesting in that the cranium OH 24 is placed at the positive extreme together with the three reconstructions of KNM-ER 1470 and the three australopithecine crania are at the negative extreme. On PCIII Sts 5 is close to KNM-ER 406, on PCIV it is close to OH 5 and on PCV all australopithecines are close. On the higher PCs (III,IV & V) the specimens which have been attributed to early *Homo* are more randomly distributed.

Scaled data

An identical series of PCAs to those described using 34 raw variables was carried out using 34 variables which were adjusted by ratio against the square root of the midline area of each cranium. The equivalent plots of the scores of individuals on the first few PCs are presented in figures B.10 to B.18. In table B.2a are presented the proportions of the total variance which are accounted

for by the first five PCs from each analysis. Table B.2b lists the correlations of the square root of the midline area with the scores of individuals on these first five components.

Table B.3 lists the Euclidean distances between fossil crania calculated from the 34 scaled variables.

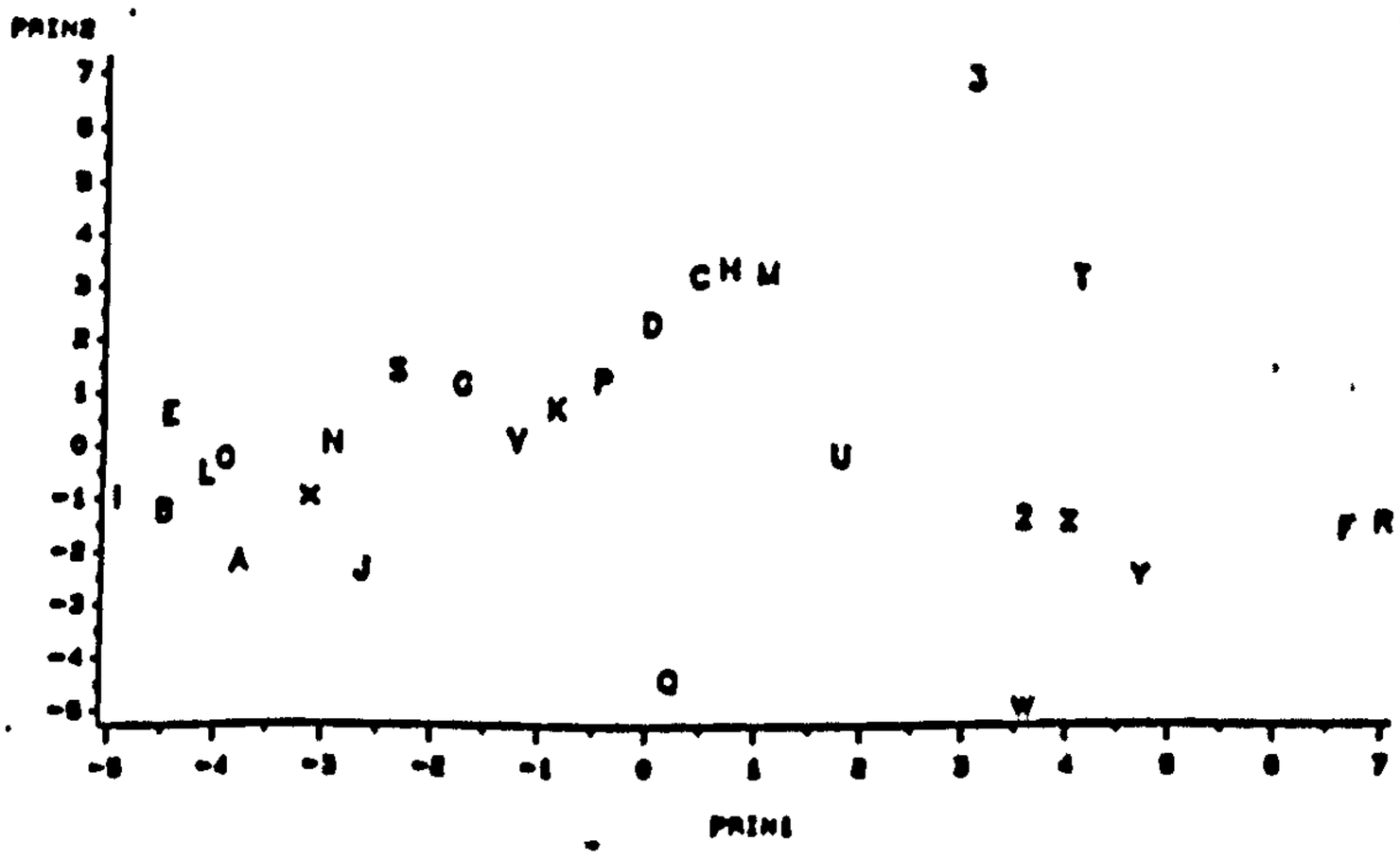
Plots of the scores of fossil and modern crania on canonical axes calculated from 34 scaled variables are presented in figures B.19 and B.20.

*a. PCA of all Fossil crania*

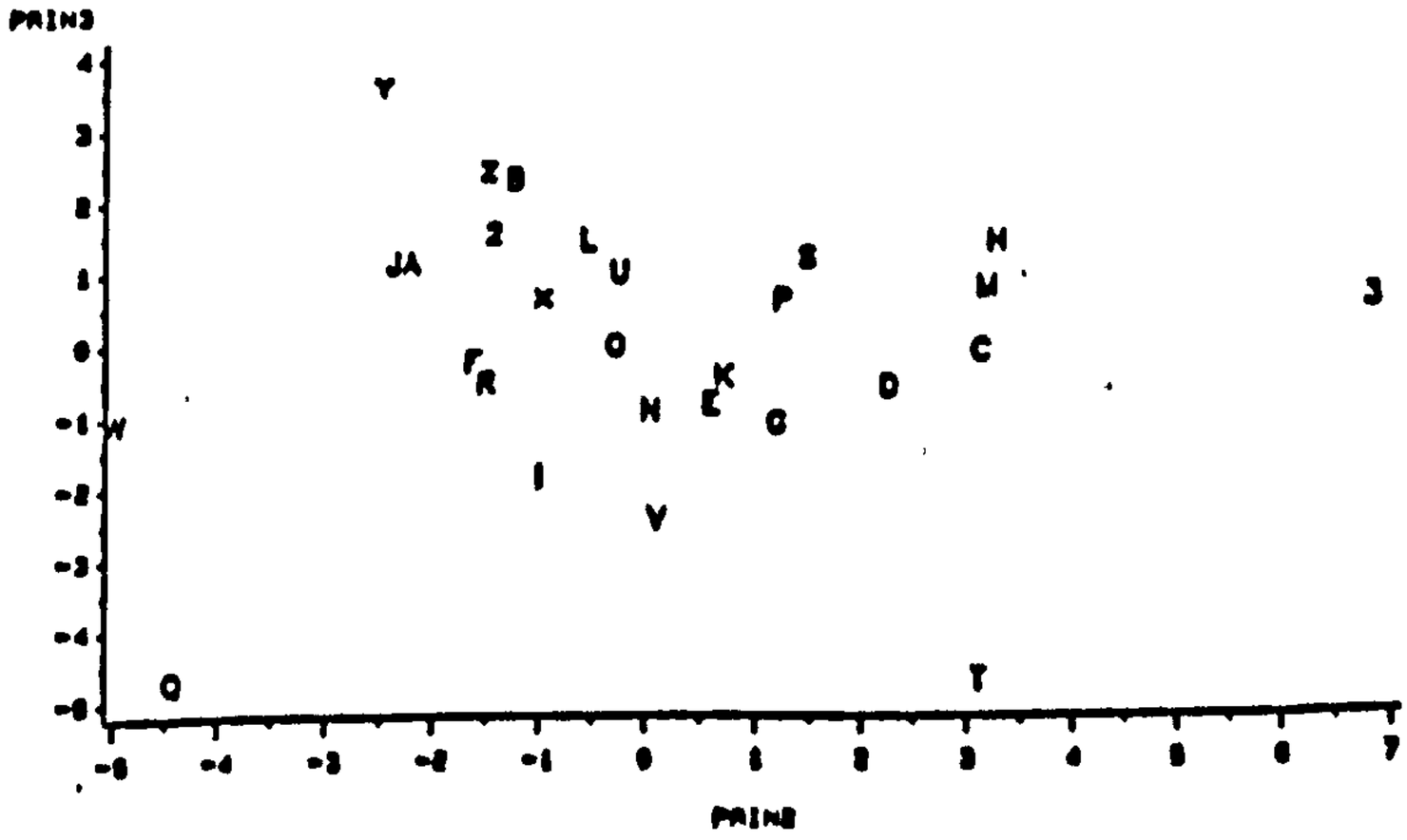
In figure B.10 are presented plots of the scores of crania on the first 4 PCs of the analysis which used scaled data from all of the fossil material. At first glance the plot of PCI vs PCII (55% of total variance) appears radically different from that of figure B.1 which used raw data. However this appearance is largely due to the fact that the scores of the crania on the first PC are reversed. When allowance is made for this the relationships between the crania are generally similar to those in fig B.1. The scores of crania on the first PC have a marked correlation with the size variable (table B.2b – $r = -0.70$, $P < 0.001$) despite the fact that simple size has been removed from the data. This reflects the fact that a general trend in human evolution has been an increase in brain volume which has been associated with a change in cranial shape. A number of clusters are apparent from figure B.10a (PCI vs PCII). The largest is placed towards the negative pole of PCI and centrally on PCII. It includes all of the fossils which have been attributed to archaic and modern

FIGURE B.10 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)




c)

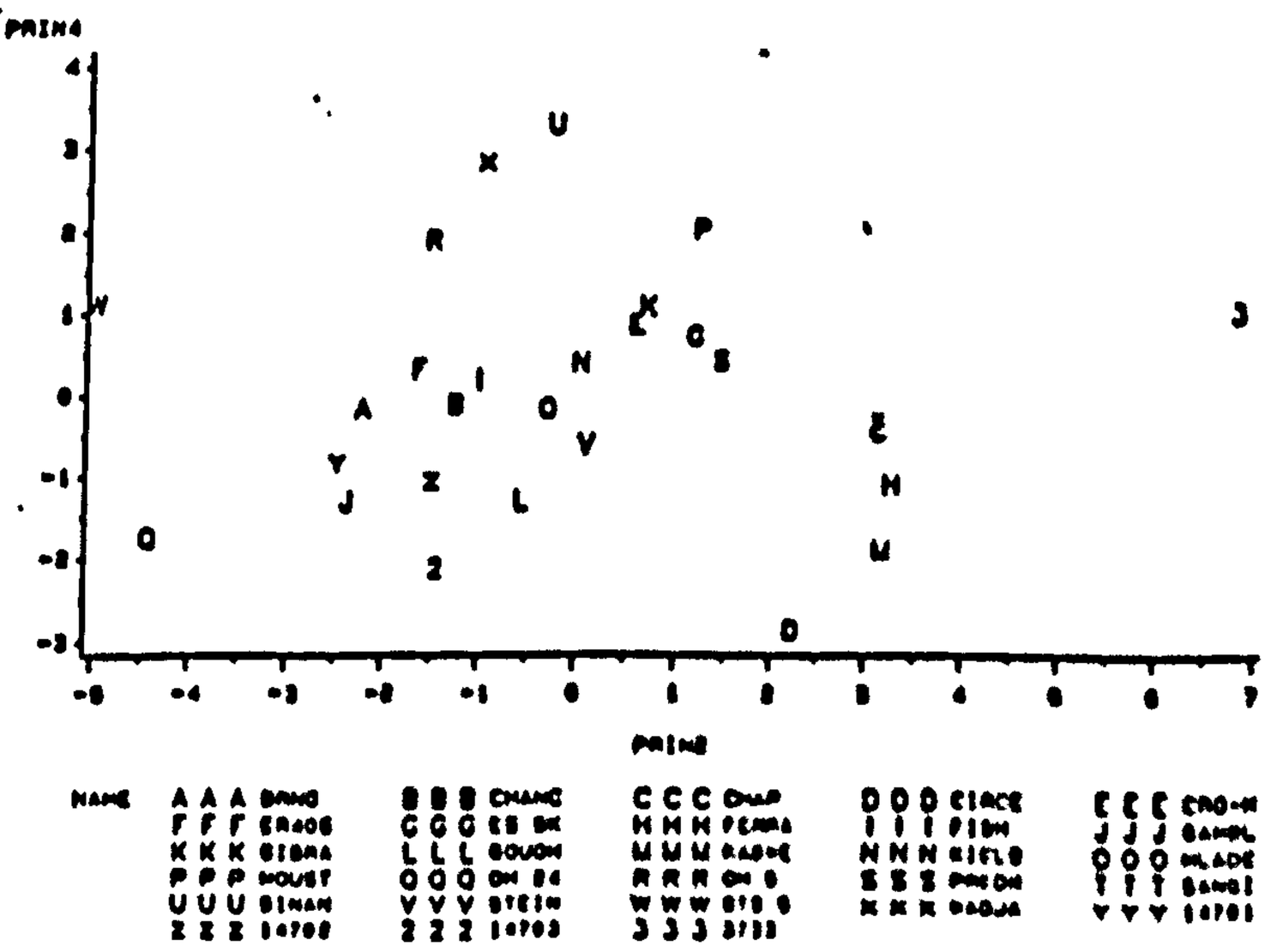



Fig B.10

## TABLE B2

### Principal component analyses of 34 scaled variables

a. The cumulative proportion of the total variance expressed on each PC (%)

| PC | I | II | III | IV | V |
|---|---|---|---|---|---|
| GROUP | | | | | |
| All Fossils | 37 | 55 | 66 | 72 | 78 |
| *H. Sap.* subsp. | 36 | 50 | 60 | 71 | 80 |
| a.m. *H. Sap.* | 26 | 49 | 66 | 76 | 85 |
| Neanderthals + archaic *H.sap* | 32 | 53 | 70 | 82 | 91 |
| Apiths + *H.hab.* | 37 | 64 | 83 | 95 | 98 |

b. The correlation of the size variable with individual scores on PCs I – V

| PC | I | II | III | IV | V |
|---|---|---|---|---|---|
| GROUP | | | | | |
| All Fossils | −0.70** | 0.22 | 0.25 | 0.00 | 0.08 |
| *H. Sap.* subsp. | 0.08 | 0.05 | −0.22 | 0.31 | 0.75** |
| a.m. *H. Sap.* | 0.48 | −0.35 | 0.38 | 0.17 | 0.29 |
| Neanderthals + archaic *H. Sap.* | 0.79** | 0.49 | −0.21 | 0.15 | 0.05 |
| Apiths + *H. hab.* | 0.91** | 0.37 | 0.00 | −0.13 | 0.09 |

P < 0.01 = **
Others are NS

TABLE B.3

EUCLIDEAN DISTANCE MATRIX

Calculated from scaled data

| | CRO-MA | GAMBLE | GOUGHS | CHANCE | PREDMO | BRNO 3 | MLADEC |
|---|---|---|---|---|---|---|---|
| CRO-MAGNON 1 | 0.0 | 66.4 | 45.2 | 44.4 | 25.4 | 45.2 | 21.6 |
| GAMBLES CAVE 4 | 66.4 | 0.0 | 40.7 | 43.4 | 64.5 | 46.1 | 54.9 |
| GOUGHS CAVE 1 | 45.2 | 40.7 | 0.0 | 18.4 | 45.4 | 25.0 | 33.3 |
| CHANCELADE 1 | 44.4 | 43.4 | 18.4 | 0.0 | 42.3 | 26.5 | 33.0 |
| PREDMOST 3 | 25.4 | 64.5 | 45.4 | 42.3 | 0.0 | 45.5 | 24.5 |
| BRNO 3 | 45.2 | 46.1 | 25.0 | 26.5 | 45.5 | 0.0 | 29.8 |
| MLADEC 1 | 21.6 | 54.9 | 33.3 | 33.0 | 24.5 | 29.8 | 0.0 |
| FISH HOEK 1 | 42.9 | 46.0 | 44.0 | 47.6 | 52.6 | 46.2 | 40.4 |
| KEILOR 1 | 28.7 | 57.3 | 41.5 | 41.6 | 29.8 | 37.9 | 23.8 |
| WADJAK 1 | 44.8 | 49.1 | 49.0 | 46.9 | 40.6 | 47.5 | 39.2 |
| MOUSTIER 1 | 50.0 | 67.2 | 57.0 | 57.5 | 40.3 | 56.8 | 46.4 |
| CHAPELLE A.S. | 53.5 | 70.6 | 63.0 | 65.1 | 40.3 | 65.5 | 48.2 |
| FERRASIE 1 | 52.9 | 63.0 | 56.5 | 59.1 | 39.1 | 62.7 | 50.5 |
| CIRCEO 1 | 50.0 | 61.0 | 54.4 | 60.0 | 44.4 | 60.8 | 48.1 |
| GIBRALTAR 1 | 48.1 | 50.0 | 53.4 | 53.7 | 42.0 | 57.0 | 44.2 |
| SKHUL 5 | 30.4 | 66.0 | 54.3 | 54.6 | 27.0 | 49.8 | 29.7 |
| KABWE | 50.2 | 56.5 | 53.6 | 55.1 | 39.1 | 59.5 | 46.8 |
| SINANTHROPUS | 65.5 | 74.7 | 73.2 | 71.2 | 51.5 | 74.0 | 61.9 |
| SANGIRAN 4 | 83.9 | 90.3 | 96.2 | 99.3 | 81.1 | 101.0 | 86.0 |
| STS 5 | 98.3 | 91.7 | 96.8 | 95.9 | 92.8 | 89.1 | 88.5 |
| OH 24 | 84.9 | 69.2 | 82.0 | 88.4 | 89.4 | 75.3 | 77.9 |
| OH 5 | 104.6 | 103.7 | 112.7 | 110.9 | 93.8 | 108.6 | 101.0 |
| ER 406 | 108.4 | 101.9 | 109.0 | 109.0 | 98.5 | 108.5 | 102.3 |
| 14701 | 96.3 | 76.6 | 83.9 | 82.0 | 82.3 | 83.0 | 85.4 |
| 14702 | 75.6 | 71.3 | 72.2 | 70.8 | 62.1 | 69.1 | 67.7 |
| 14703 | 71.8 | 67.0 | 70.3 | 70.9 | 60.6 | 67.8 | 65.3 |
| STEINHEIM 1 | 36.7 | 69.8 | 55.6 | 58.1 | 40.3 | 48.9 | 35.8 |
| 3733 | 75.8 | 108.6 | 96.4 | 97.8 | 64.6 | 99.3 | 81.0 |

| | FISH H | KEILOR | WADJAK | MOUSTI | CHAPEL | FERRAS | CIRCEO |
|---|---|---|---|---|---|---|---|
| CRO-MAGNON 1 | 42.9 | 28.7 | 44.8 | 50.0 | 53.5 | 52.9 | 50.0 |
| GAMBLES CAVE 4 | 46.0 | 57.3 | 49.1 | 67.2 | 70.6 | 63.0 | 61.0 |
| GOUGHS CAVE 1 | 44.0 | 41.5 | 49.0 | 57.0 | 63.0 | 56.5 | 54.4 |
| CHANCELADE 1 | 47.6 | 41.6 | 46.9 | 57.5 | 65.1 | 59.1 | 60.0 |
| PREDMOST 3 | 52.6 | 29.8 | 40.6 | 40.3 | 40.3 | 39.1 | 44.4 |
| BRNO 3 | 46.2 | 37.9 | 47.5 | 56.8 | 65.5 | 62.7 | 60.8 |
| MLADEC 1 | 40.4 | 23.8 | 39.2 | 46.4 | 48.2 | 50.5 | 48.1 |
| FISH HOEK 1 | 0.0 | 47.5 | 41.6 | 66.0 | 66.4 | 65.3 | 56.4 |
| KEILOR 1 | 47.5 | 0.0 | 38.6 | 37.5 | 46.1 | 46.5 | 51.6 |
| WADJAK 1 | 41.6 | 38.6 | 0.0 | 50.0 | 55.0 | 52.2 | 61.7 |
| MOUSTIER 1 | 66.0 | 37.5 | 50.0 | 0.0 | 32.6 | 37.9 | 51.4 |
| CHAPELLE A.S. | 66.4 | 46.1 | 55.0 | 32.6 | 0.0 | 28.5 | 38.6 |
| FERRASIE 1 | 65.3 | 46.5 | 52.2 | 37.9 | 28.5 | 0.0 | 32.6 |
| CIRCEO 1 | 56.4 | 51.6 | 61.7 | 51.4 | 38.6 | 32.6 | 0.0 |
| GIBRALTAR 1 | 42.4 | 44.0 | 30.4 | 47.2 | 43.3 | 41.9 | 47.5 |
| SKHUL 5 | 52.2 | 28.9 | 38.9 | 46.6 | 43.6 | 46.5 | 49.7 |
| KABWE | 58.3 | 43.7 | 48.0 | 43.1 | 34.3 | 21.7 | 35.1 |
| SINANTHROPUS | 72.5 | 60.5 | 54.9 | 47.4 | 44.3 | 47.4 | 58.0 |
| SANGIRAN 4 | 86.0 | 76.9 | 83.2 | 69.3 | 59.6 | 64.2 | 64.1 |
| STS 5 | 97.6 | 89.2 | 91.9 | 87.3 | 83.4 | 89.5 | 89.3 |
| OH 24 | 67.4 | 78.1 | 79.7 | 91.9 | 88.2 | 89.9 | 77.1 |
| OH 5 | 112.1 | 95.0 | 94.5 | 86.6 | 80.5 | 82.5 | 89.1 |
| ER 406 | 112.7 | 101.2 | 100.0 | 89.6 | 84.1 | 85.6 | 88.5 |
| 14701 | 97.2 | 84.0 | 83.5 | 71.8 | 70.3 | 67.8 | 77.7 |
| 14702 | 84.3 | 65.2 | 68.3 | 59.8 | 57.4 | 52.8 | 62.8 |
| 14703 | 78.4 | 64.1 | 67.5 | 62.6 | 57.9 | 51.5 | 55.3 |
| STEINHEIM 1 | 57.0 | 32.7 | 59.2 | 46.3 | 46.6 | 52.1 | 44.3 |
| 3733 | 100.6 | 76.4 | 84.6 | 60.1 | 52.1 | 51.4 | 66.5 |

| | GIBRAL | SKHUL | KABWE | SINANT | SANGIR | STS 5 | OH 24 |
|---|---|---|---|---|---|---|---|
| CRO-MAGNON 1 | 48.1 | 30.4 | 50.2 | 65.5 | 83.9 | 98.3 | 84.8 |
| GAMBLES CAVE 4 | 50.0 | 66.0 | 56.5 | 74.7 | 90.3 | 91.7 | 69.2 |
| GOUGHS CAVE 1 | 53.4 | 54.3 | 53.6 | 73.2 | 96.2 | 96.8 | 82.0 |
| CHANCELADE 1 | 53.7 | 54.6 | 55.1 | 71.2 | 89.3 | 95.9 | 88.4 |
| PREDMOST 3 | 42.0 | 27.0 | 39.1 | 51.5 | 81.1 | 92.8 | 89.4 |
| BRNO 3 | 57.0 | 49.8 | 59.5 | 74.0 | 101.0 | 89.1 | 75.3 |
| MLADEC 1 | 44.2 | 29.7 | 46.8 | 61.9 | 86.0 | 88.5 | 77.9 |
| FISH HOEK 1 | 42.4 | 52.2 | 58.3 | 72.5 | 86.0 | 97.8 | 67.4 |
| KEILOR 1 | 44.0 | 28.9 | 43.7 | 60.5 | 76.9 | 89.2 | 78.1 |
| WADJAK 1 | 30.4 | 38.9 | 48.0 | 54.9 | 83.2 | 91.9 | 79.7 |
| MOUSTIER 1 | 47.2 | 46.8 | 43.1 | 47.4 | 69.3 | 87.3 | 91.9 |
| CHAPELLE A.S. | 43.3 | 43.6 | 34.3 | 44.3 | 59.8 | 83.4 | 88.2 |
| FERRASIE 1 | 41.9 | 46.5 | 21.7 | 47.4 | 64.2 | 89.5 | 89.9 |
| CIRCEO 1 | 47.5 | 49.7 | 35.1 | 58.0 | 64.1 | 89.3 | 77.1 |
| GIBRALTAR 1 | 0.0 | 38.9 | 35.8 | 44.2 | 62.7 | 82.8 | 72.2 |
| SKHUL 5 | 38.9 | 0.0 | 42.3 | 57.4 | 73.7 | 87.8 | 76.6 |
| KABWE | 35.8 | 42.3 | 0.0 | 49.4 | 58.8 | 83.3 | 81.7 |
| SINANTHROPUS | 44.2 | 57.4 | 49.4 | 0.0 | 64.7 | 74.7 | 89.3 |
| SANGIRAN 4 | 62.7 | 73.7 | 58.8 | 64.7 | 0.0 | 86.2 | 84.9 |
| STS 5 | 82.8 | 87.8 | 83.3 | 74.7 | 86.2 | 0.0 | 71.0 |
| OH 24 | 72.2 | 76.6 | 81.7 | 89.3 | 84.9 | 71.0 | 0.0 |
| OH 5 | 82.5 | 87.5 | 78.7 | 64.2 | 67.8 | 60.8 | 92.3 |
| ER 406 | 86.8 | 95.3 | 82.6 | 72.2 | 72.3 | 56.5 | 95.3 |
| 14701 | 75.1 | 87.9 | 67.0 | 58.6 | 86.4 | 56.9 | 92.4 |
| 14702 | 60.3 | 64.6 | 51.0 | 46.8 | 75.6 | 89.5 | 81.5 |
| 14703 | 58.1 | 60.7 | 46.8 | 50.1 | 71.9 | 62.5 | 71.9 |
| STEINHEIM 1 | 52.6 | 33.7 | 48.4 | 64.5 | 71.3 | 80.1 | 89.1 |
| 3733 | 74.6 | 65.9 | 59.2 | 66.2 | 71.8 | 109.5 | 119.4 |

| | OH 5 | ER 406 | 14701 | 14702 | 14703 | STEINH | 3733 |
|---|---|---|---|---|---|---|---|
| CRO-MAGNON 1 | 104.6 | 108.4 | 96.3 | 75.6 | 71.8 | 36.7 | 75.8 |
| GAMBLES CAVE 4 | 103.7 | 101.9 | 76.6 | 71.3 | 67.0 | 69.8 | 108.6 |
| GOUGHS CAVE 1 | 112.7 | 109.0 | 83.9 | 72.2 | 70.3 | 85.6 | 96.4 |
| CHANCELADE 1 | 110.9 | 109.0 | 82.0 | 70.6 | 70.9 | 58.1 | 97.8 |
| PREDMOST 3 | 93.8 | 98.5 | 82.3 | 62.1 | 60.6 | 40.3 | 64.6 |
| BRNO 3 | 108.6 | 108.5 | 83.0 | 69.1 | 67.8 | 48.9 | 99.3 |
| MLADEC 1 | 101.0 | 102.3 | 85.4 | 67.7 | 65.3 | 35.5 | 81.0 |
| FISH HOEK 1 | 112.1 | 112.7 | 97.2 | 84.3 | 78.4 | 57.0 | 100.6 |
| KEILOR 1 | 95.0 | 101.2 | 84.0 | 65.2 | 64.1 | 32.7 | 76.4 |
| WADJAK 1 | 94.5 | 100.0 | 83.5 | 68.3 | 67.5 | 59.2 | 84.6 |
| MOUSTIER 1 | 86.6 | 89.6 | 71.8 | 59.8 | 62.6 | 46.3 | 60.1 |
| CHAPELLE A.S. | 80.5 | 84.1 | 70.3 | 57.4 | 57.9 | 46.6 | 52.1 |
| FERRASIE 1 | 82.5 | 85.6 | 67.8 | 52.8 | 51.5 | 52.1 | 51.4 |
| CIRCEO 1 | 89.1 | 88.5 | 77.7 | 62.8 | 55.3 | 44.3 | 66.5 |
| GIBRALTAR 1 | 82.5 | 86.8 | 75.1 | 60.3 | 58.1 | 52.6 | 74.6 |
| SKHUL 5 | 87.5 | 95.3 | 87.9 | 64.6 | 60.7 | 33.7 | 65.9 |
| KABWE | 78.7 | 82.6 | 67.0 | 51.0 | 46.8 | 48.4 | 59.2 |
| SINANTHROPUS | 64.2 | 72.2 | 58.6 | 46.8 | 50.1 | 64.5 | 66.2 |
| SANGIRAN 4 | 67.8 | 72.3 | 86.4 | 75.6 | 71.9 | 71.3 | 71.8 |
| STS 5 | 60.8 | 56.5 | 56.9 | 89.5 | 62.5 | 80.1 | 109.5 |
| OH 24 | 92.3 | 95.3 | 92.4 | 81.5 | 71.9 | 69.1 | 119.4 |
| OH 5 | 0.0 | 43.1 | 64.4 | 56.3 | 57.5 | 89.3 | 87.2 |
| ER 406 | 43.1 | 0.0 | 63.7 | 65.2 | 66.5 | 95.1 | 95.6 |
| 14701 | 64.4 | 63.7 | 0.0 | 32.6 | 43.3 | 84.7 | 97.9 |
| 14702 | 56.3 | 65.2 | 32.6 | 0.0 | 18.1 | 63.8 | 79.7 |
| 14703 | 57.5 | 66.5 | 43.3 | 18.1 | 0.0 | 59.0 | 79.8 |
| STEINHEIM 1 | 89.3 | 95.1 | 84.7 | 63.8 | 59.0 | 0.0 | 71.5 |
| 3733 | 87.2 | 95.6 | 97.9 | 79.7 | 79.8 | 71.5 | 0.0 |

*Homo sapiens*. At one extreme are placed all of the Neanderthal and archaic *Homo sapiens* fossils and at the other all of the crania of more modern aspect. The bridge between these two groups is made up of the crania from es-Skhul and Steinheim.

Another, smaller cluster consists of the three reconstructions of KNM-ER 1470 and a separate, tight, cluster contains OH 5 and KNM-ER 406. OH 24 is distant from both of these clusters as is Sts 5. These results concord with those obtained using raw data except that the Neanderthal and archaic *Homo sapiens* fossils are more clearly distinguishable from the more modern crania. A major difference in result, however, is that the three specimens of the grade of *Homo erectus* are widely separated. This result is in agreement with the relatively large Euclidean distance between these crania (table B.3). Principal components III and IV account for 11% and 6%, respectively, of the total within group variability and exhibit variation with no clear biological meaning.

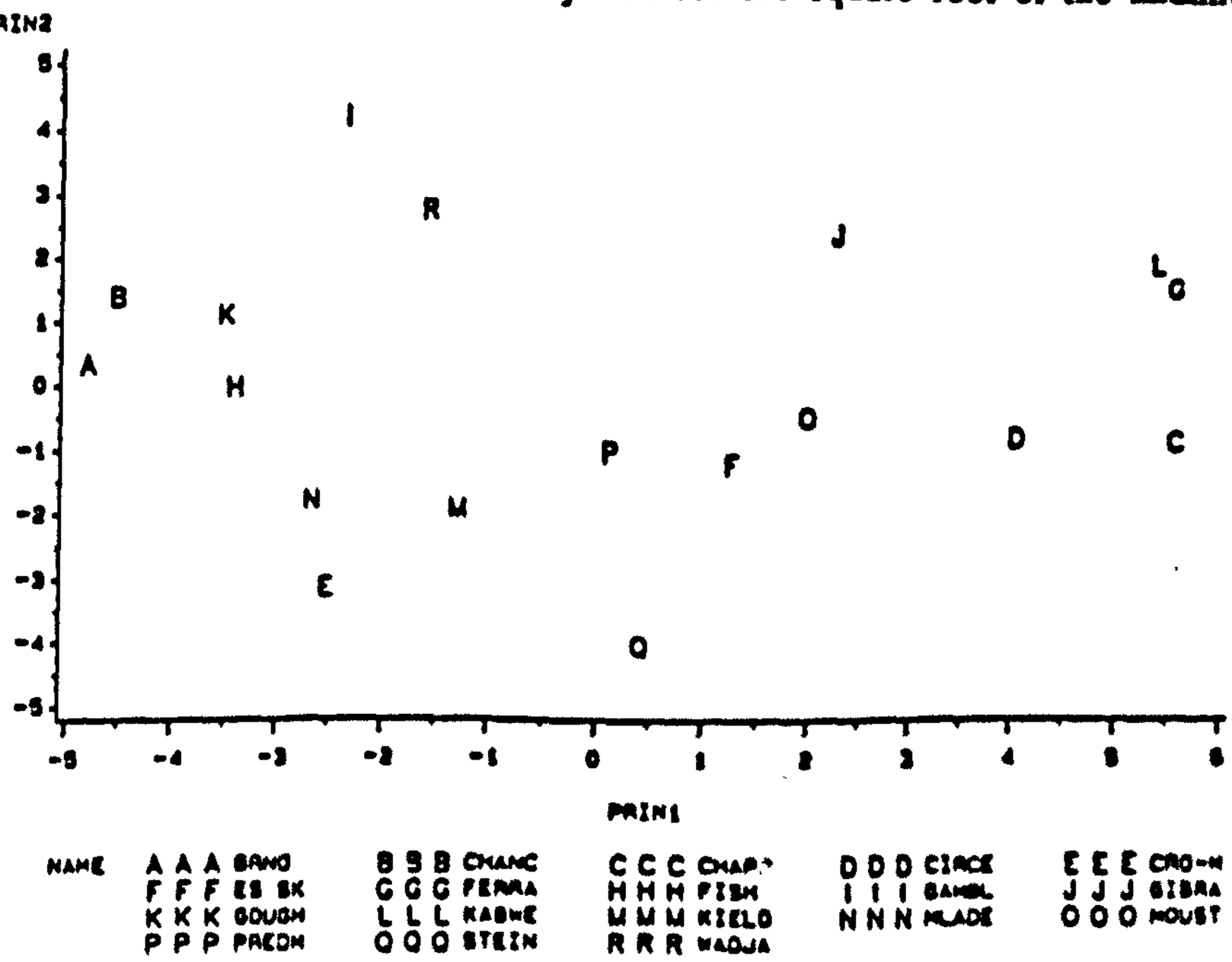
The remaining studies using scaled data have concentrated on two aspects, first the differences between the Neanderthal, Neanderthal-like and more modern human crania second the examination of shape differences within identifiable phenetic groups.

*b. Archaic and recent Homo sapiens*

Figures B.11 and B.12 present plots from the PCA of the large cluster containing the subspecies of *Homo sapiens*. There is no significant correlation between the scores of fossils on the first 3 PCs and the size variable (table

FIGURE B.11 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)

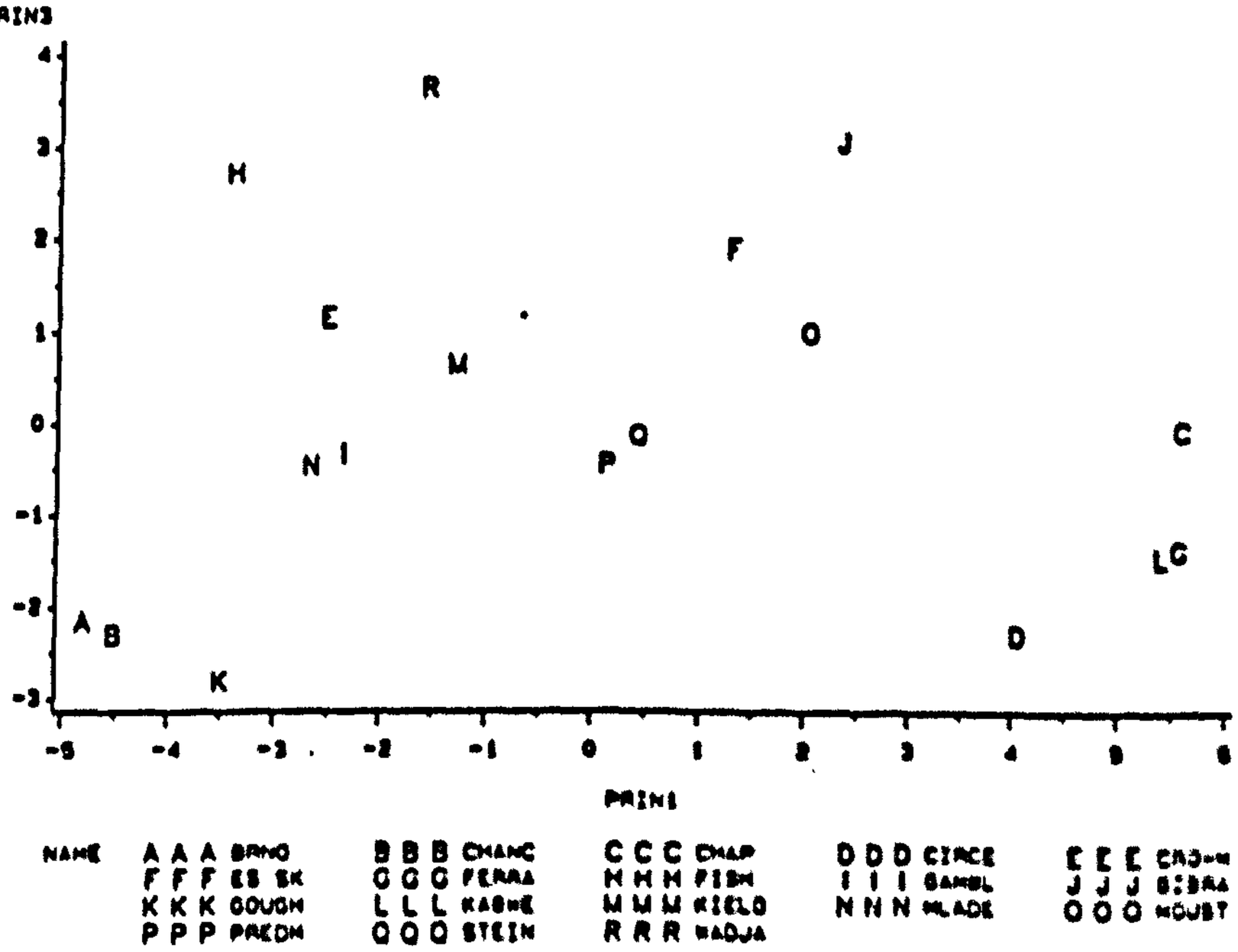
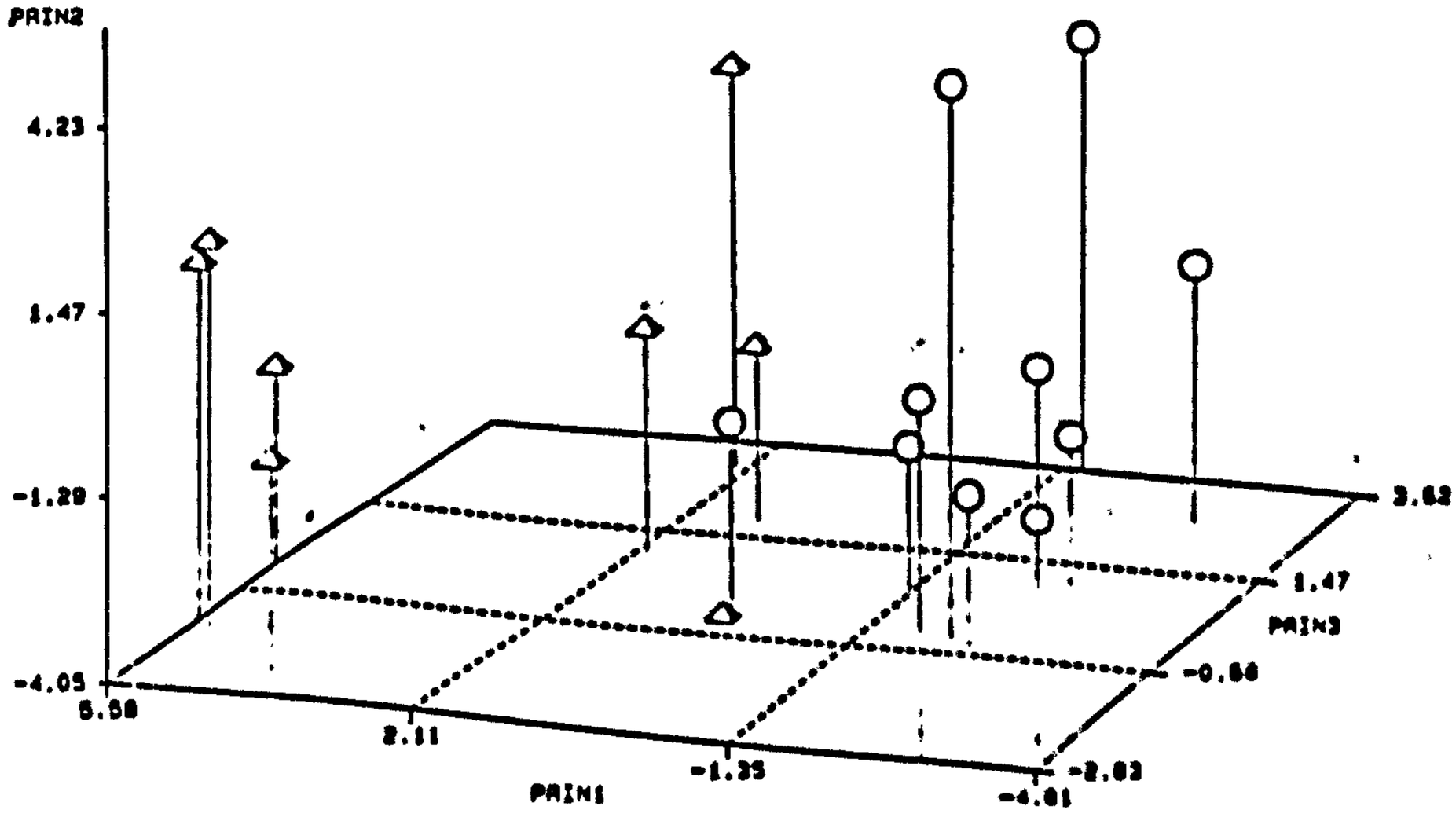



Fig B.11

FIGURE B.12 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




Key:– Pyramids = Neanderthals + Neanderthals–like crania
Circles = a.m. crania

b)

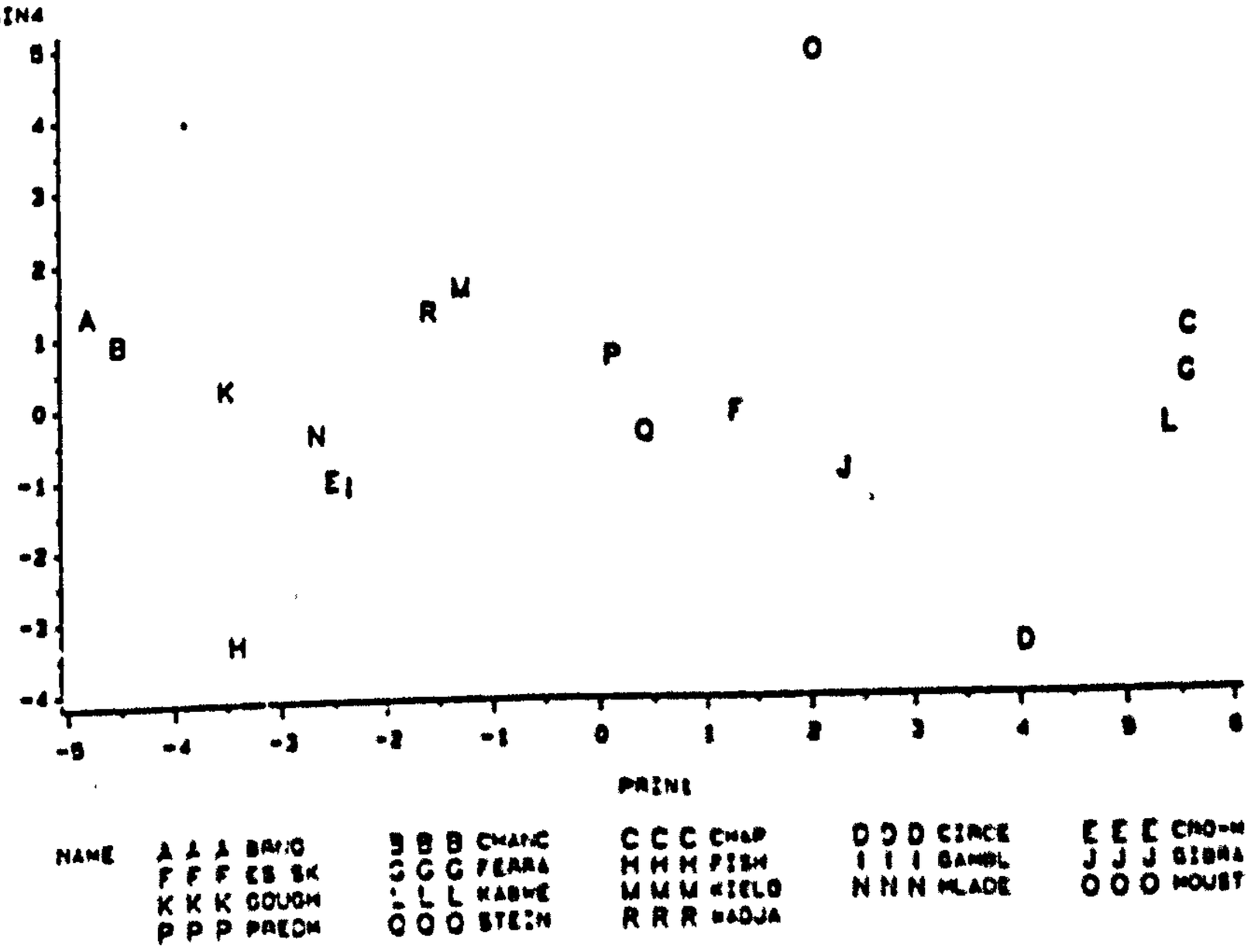



Fig B.12

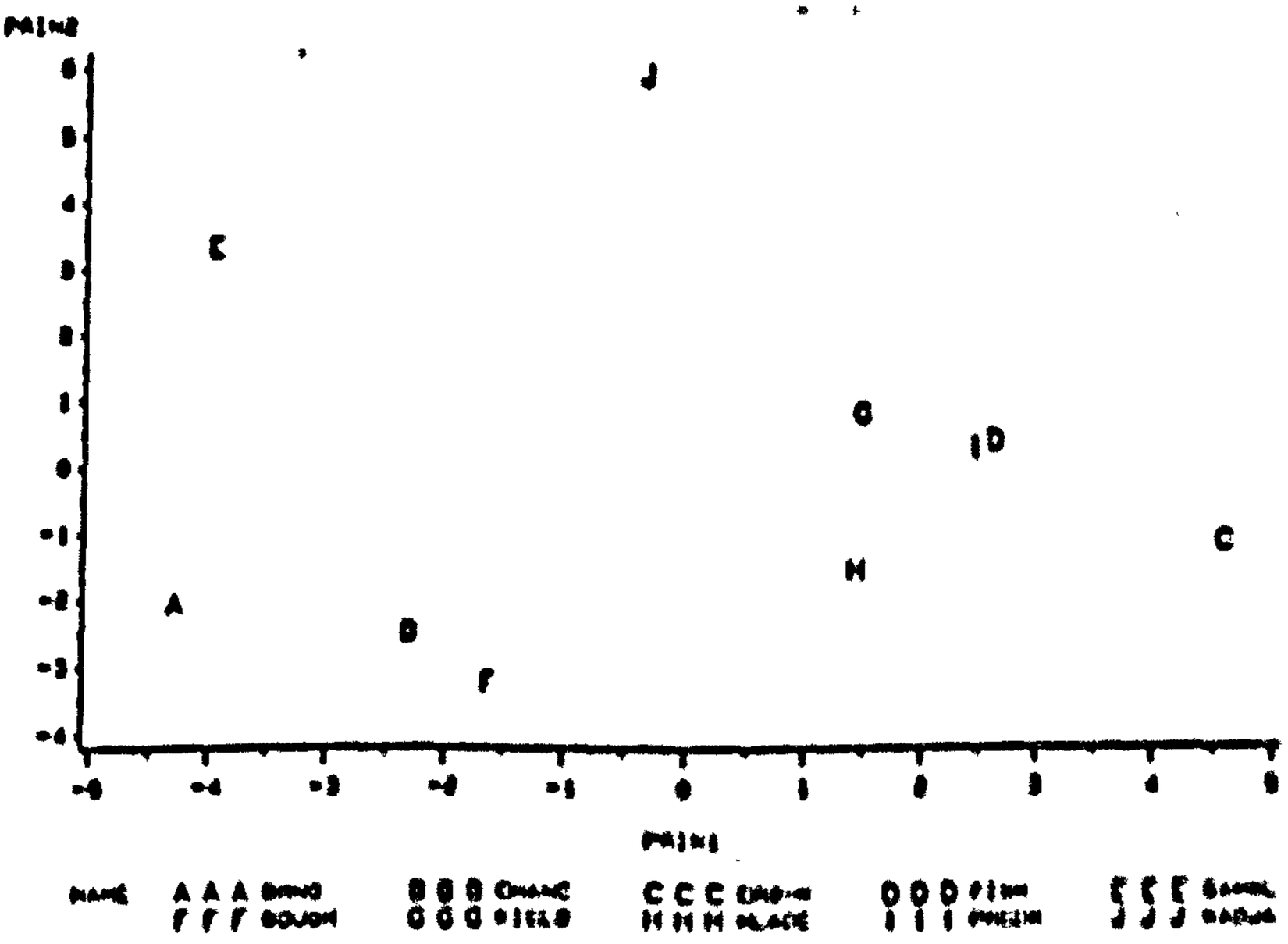
B2b). In sharp contrast to the study using raw data a clear separation is observed on PCI between the more modern crania and the Neanderthal and archaic forms. Modern crania occupy the negative pole whilst the remainder occupy the positive. The Steinheim cranium occupies an intermediate position and is immediately flanked by the crania from Predmost on the negative side and Skhul V on the positive. Within the more recent fossils of *Homo sapiens* PCII serves to distinguish the Gamble's cave 4 and Wadjak 1 crania and PCIII the Wadjak 1 and Fish Hoek 1 crania. PCIV (fig B.12b) clearly separates the adolescent Le Moustier cranium from the rest. In the three dimensional plot of PCs I vs II vs III (fig. B.12a) the Neanderthals and archaic *Homo sapiens* are marked by pyramids, a.m. fossils by circles. The demarcation between them is emphasised. The Euclidean distance matrix generally confirms the pattern of similarities indicated by the PCAs. On average the Steinheim cranium is equidistant from the "classic" Neanderthals and fossil a.m. humans and the Skhul V cranium is slightly nearer to the fossil a.m. humans than to the "classic" Neanderthals.

*c. Recent fossils of Homo sapiens*

Figures B.13 and B.14 present the plots from the PCAs of the more recent fossils of *Homo sapiens*. The study of scaled data generally repeats the results of the study of raw data. The fossils from Europe and those from a wider geographical distribution are not clearly separated on PCI. In fact, PCI seems to show a scatter of crania which has little obvious biological meaning (there is a small but non-significant correlation of scores of crania on this PC

FIGURE B.13 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)

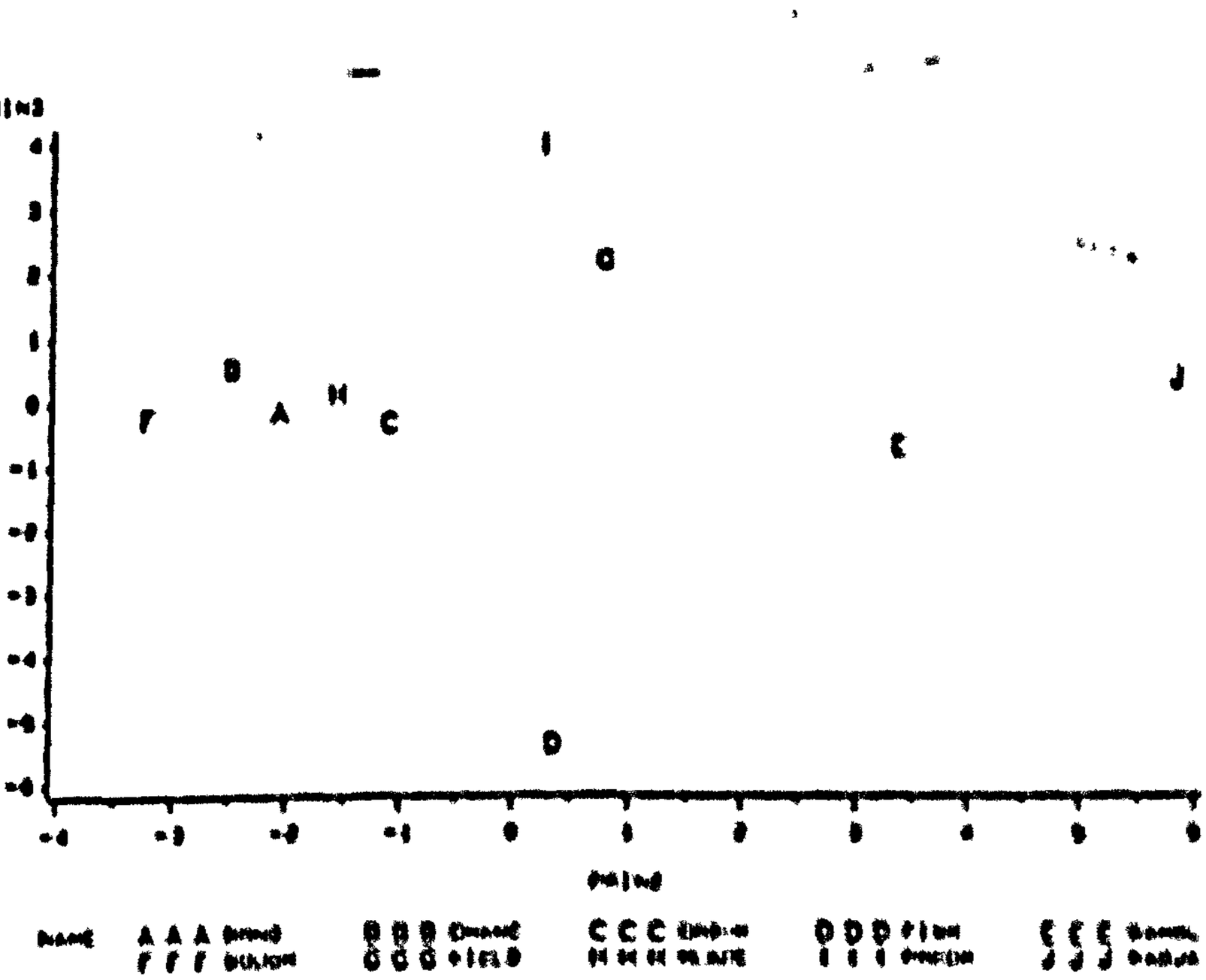
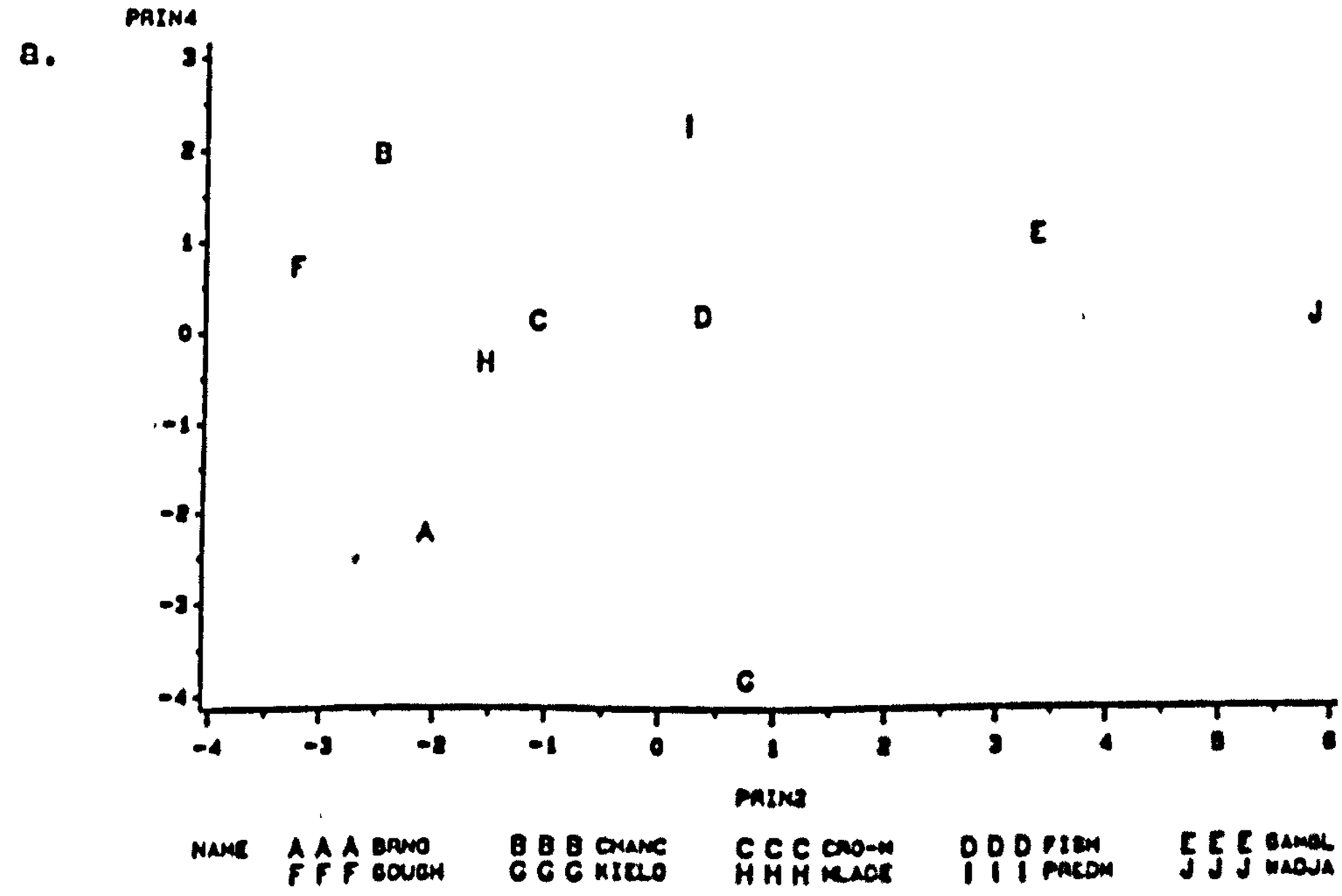



Fig B.13

FIGURE B.14 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)

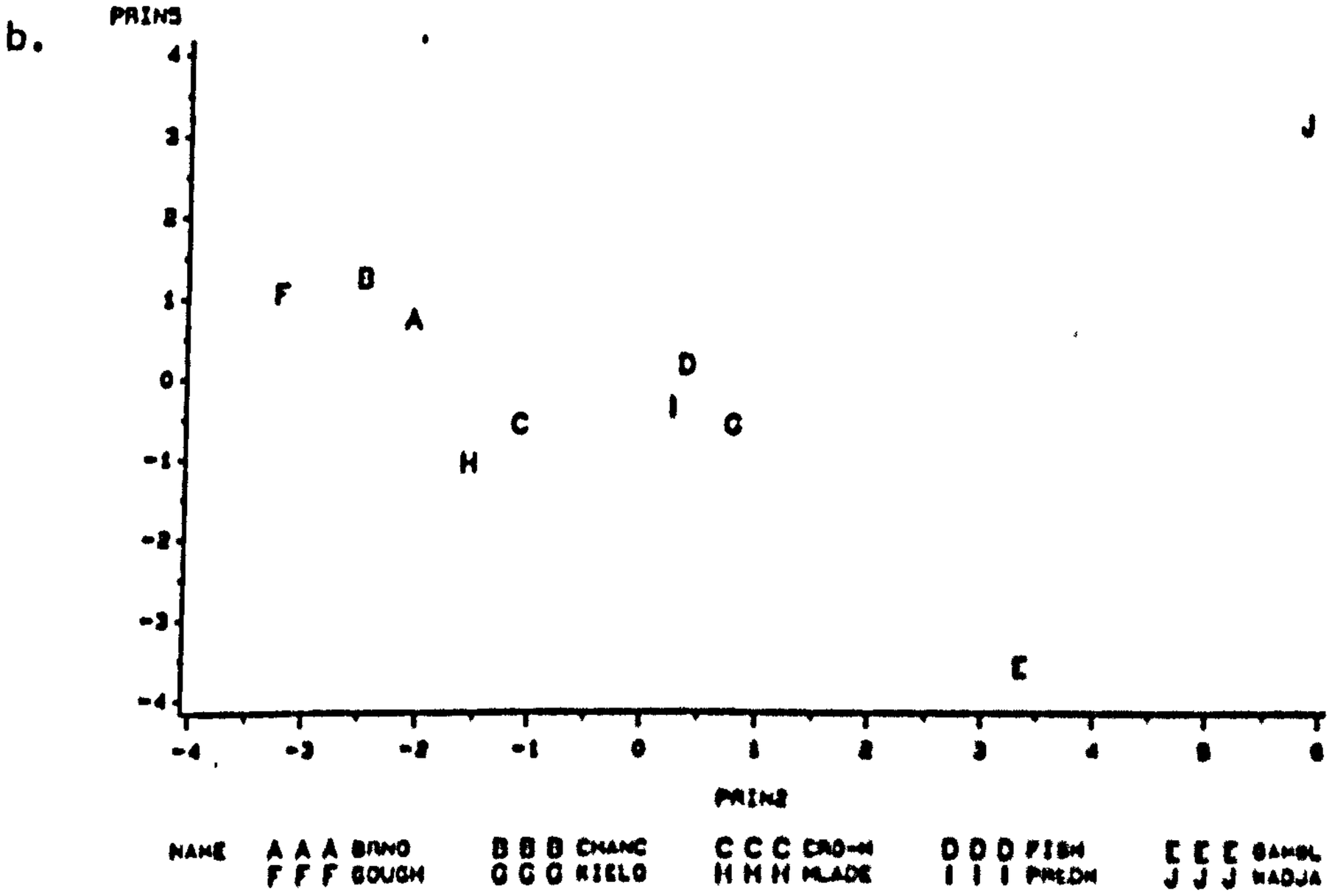



Fig B.14

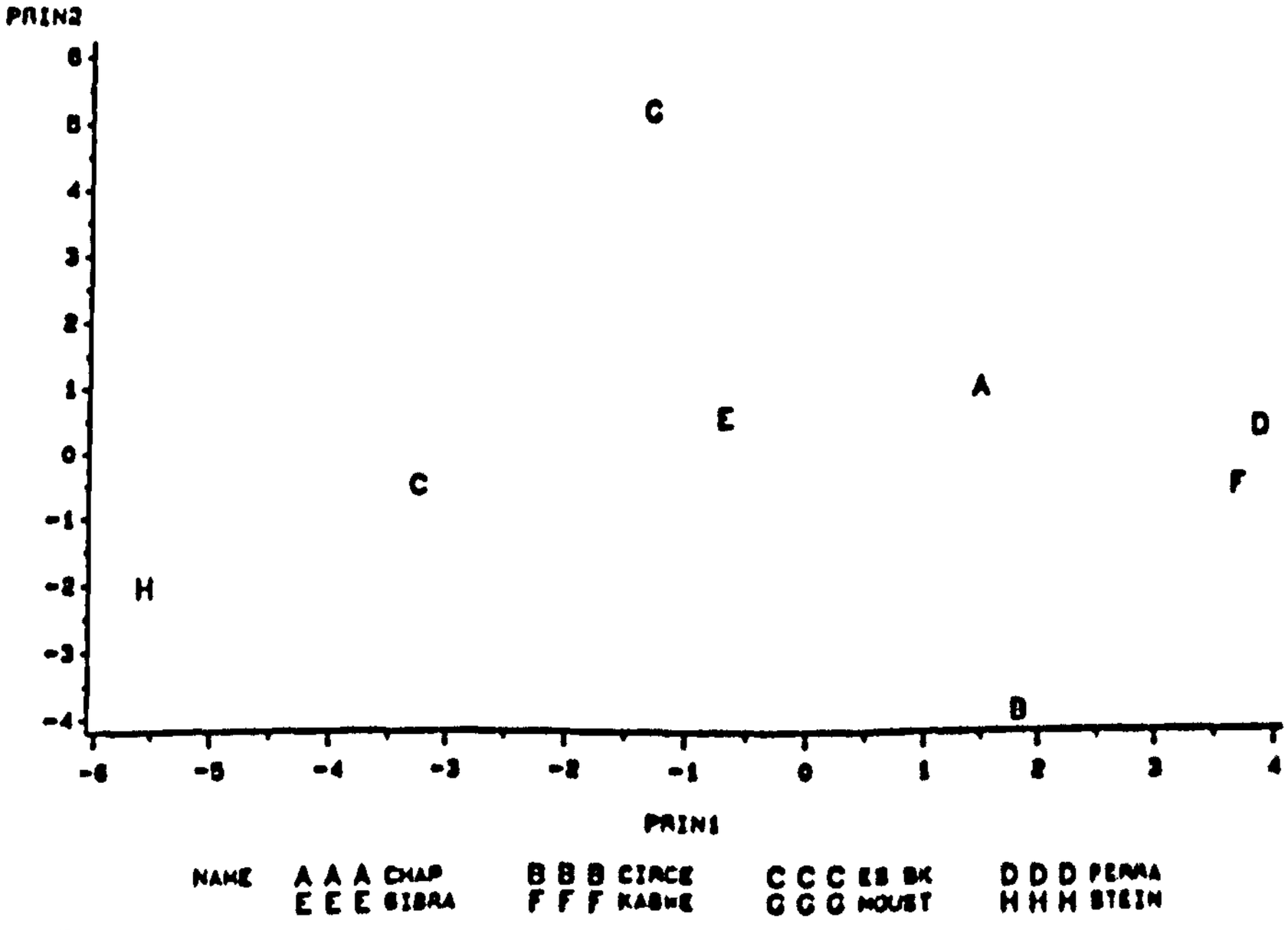
with their size variable, table B2). It accounts for only 26% of the total within group variance. PCII accounts for 23% and demarcates the European fossils on its negative pole from the others on its positive pole. On this component, however, the Fish Hoek and Keilor crania are very close to the cranium from Predmost. The higher PCs do, however, give the impression of distinctiveness in certain fossils: Fish Hoek 1 is distinctive on PC III, Keilor 1 on PC IV, and Wadjak 1 and Gamble's cave 4 occupy extreme positions on opposite poles of PC V.

*d. Neanderthals, Kabwe 1, Skhul V and the Steinheim cranium*

Figures B.15 and B.16 present the results of PCA of this group of fossils. Scores on PCI correlate 0.79 ($P<0.001$) with the size variable. At its negative extreme is the Steinheim cranium which is quite distinct from the remainder. Intermediate between it and the "classic" Neanderthals is the Skhul V cranium. At the other extreme of PCI lies the La Ferrassie 1 cranium. It is likely that the size variable correlates so highly with scores on this component because of the different cranial morphology which characterises the larger Neanderthals (see chapter 3). PCII separates the adolescent cranium, Le Moustier 1, from the rest of the crania, again (see raw data analysis) the Monte Circeo cranium occupies the opposite pole of this component. Some of the higher components (fig B.16) serve to distinguish certain crania (e.g. PCV distinguishes Kabwe 1 at one extreme and La Chapelle 1 at the other) and others show no clear pattern (e.g. III and IV). This analysis, like that using the raw data, has failed to show a

FIGURE B.15 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)

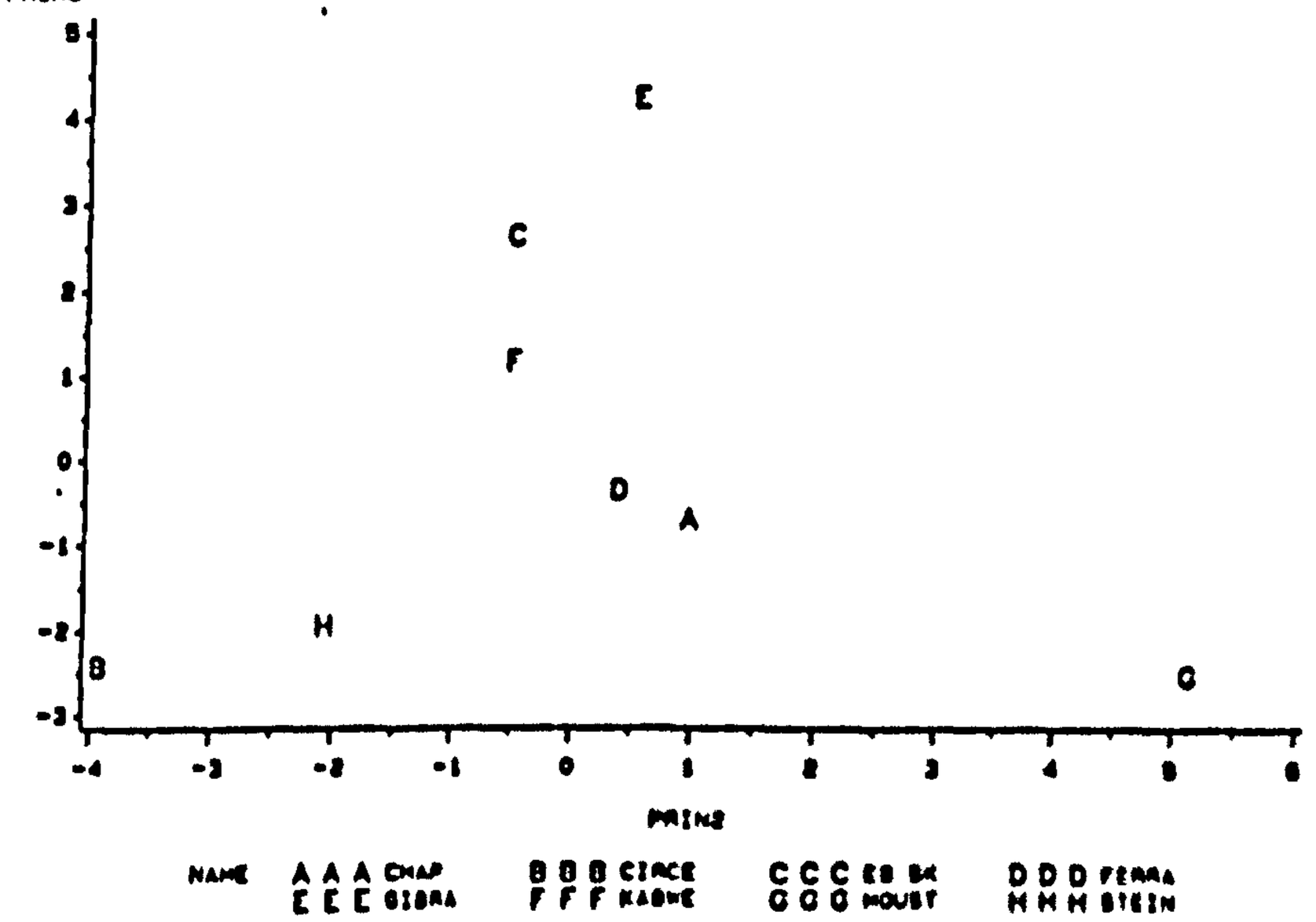
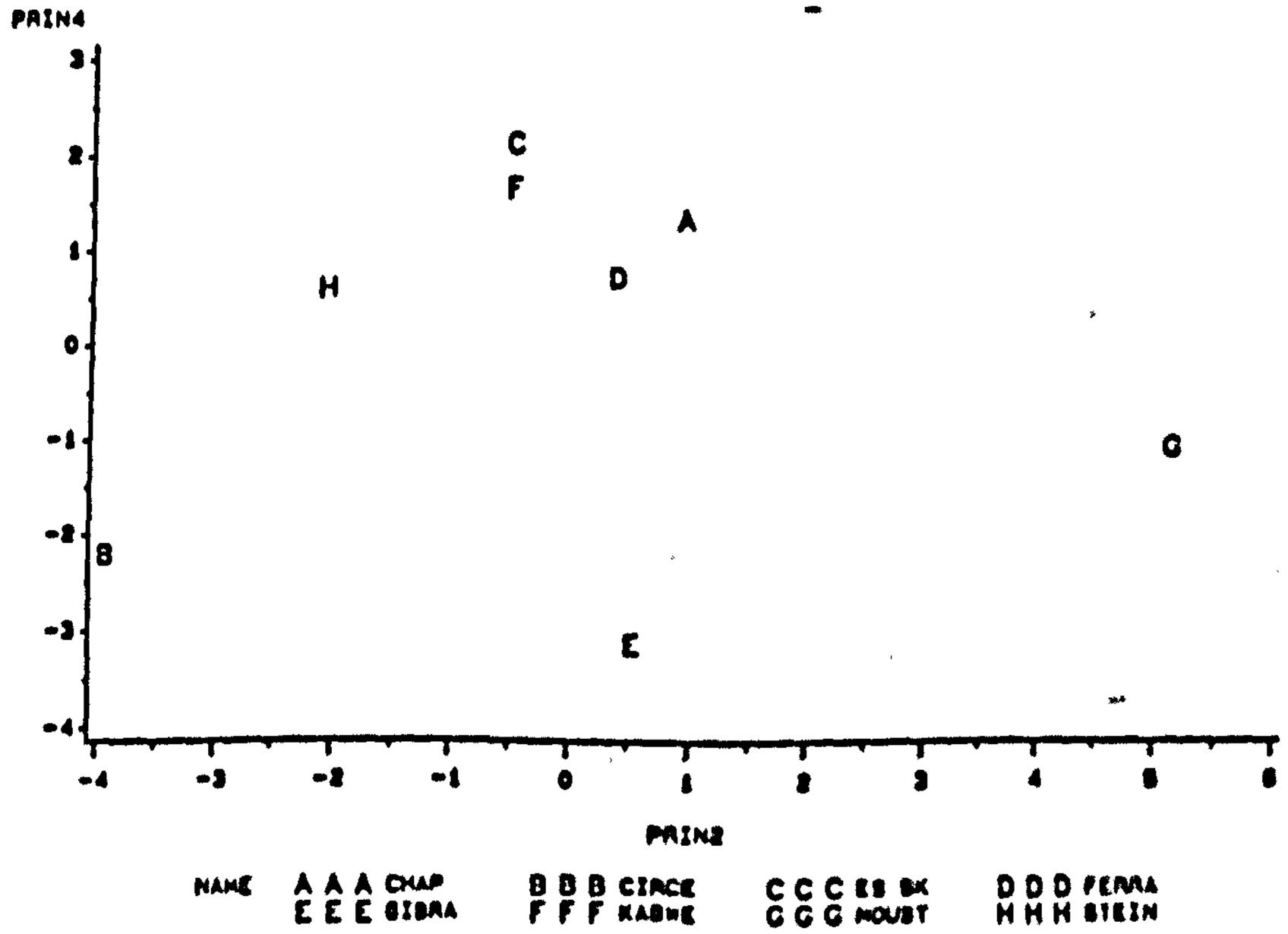



Fig B.15

FIGURE B.16 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)

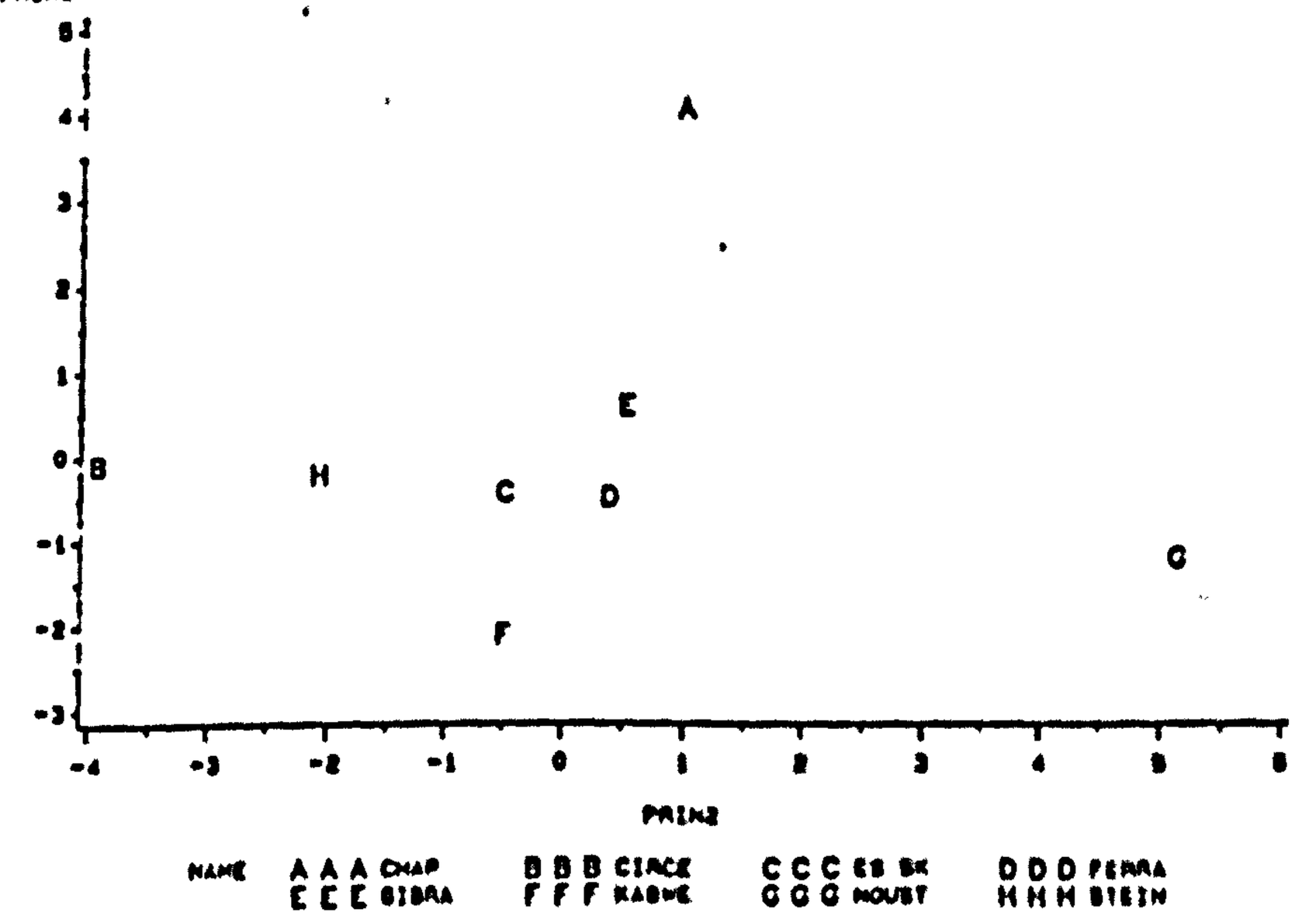



Fig B.16

clear difference between the Kabwe cranium (from Zambia) and the European Neanderthals.

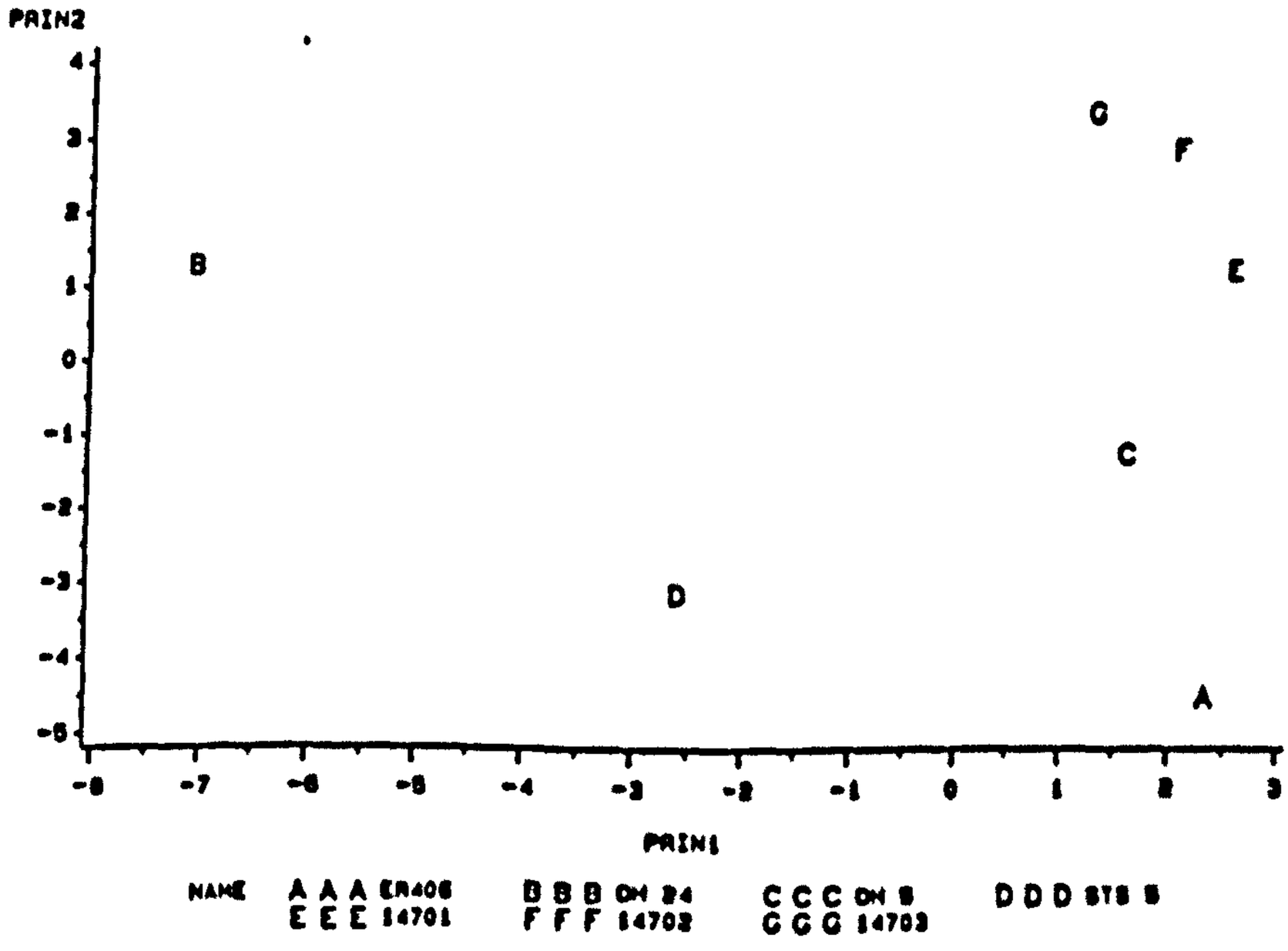
The Euclidean distance matrix also indicates that the Kabwe cranium is very similar to the "classic" Neanderthals and is most similar to the La Ferrassie 1 cranium (table, B.3, 21.7).

*e. Australopithecines and early Homo*

The plots of scores on principal components I–V are presented in figures B.17 and B.18. The results of the analysis of scaled data are remarkably similar to those that were presented earlier from raw data (representatives of early *Homo* cluster on PCII and Sts 5 is close to KNM–ER 406 on PCIII, to OH 5 on PCIV and to both on PCII). The size variable has a large correlation with scores on PCI ($r=0.91$, $P<0.001$), despite the fact that data have been scaled. As a consequence the robust australopithecines (OH 5 and KNM–ER 406) occupy one pole whilst OH 24 and Sts 5 occupy the other. The three reconstructions of KNM–ER 1470 are close to the representatives of *A. boisei* on PC I though PC II which accounts for a significant proportion of total within group variability (PCI = 37%, PCII = 27%) clearly separates early *Homo* from the australopithecines. The three reconstructions of KNM–ER 1470 appear somewhat scattered on the higher components (esp. PCV) but the spread of these reconstructions is of the same order as that between the representatives of *A. boisei*.

FIGURE B.17 – Principal Components Analysis of 34 scaled linear and angular dimensions adjusted for the square root of the midline area

a)




b)

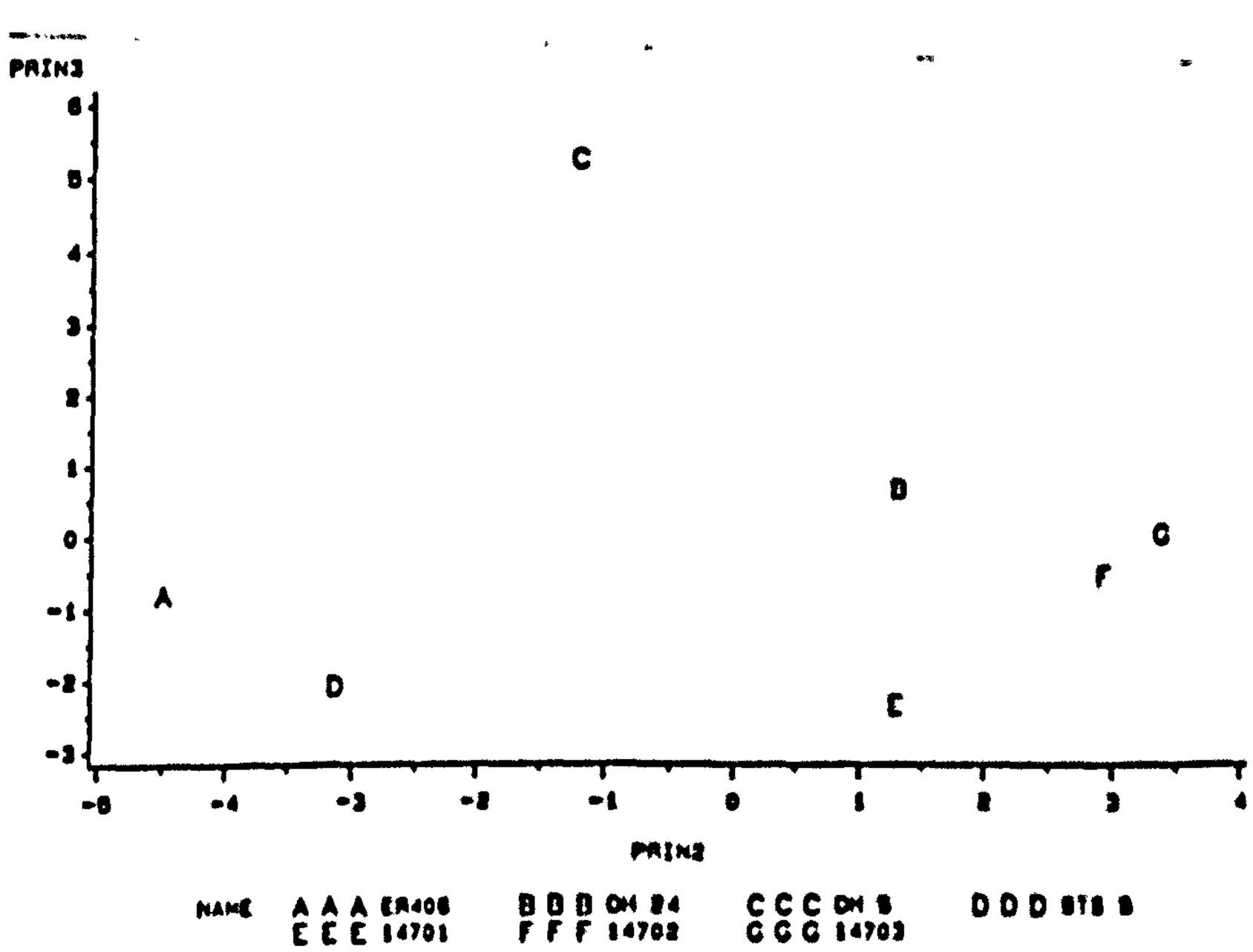
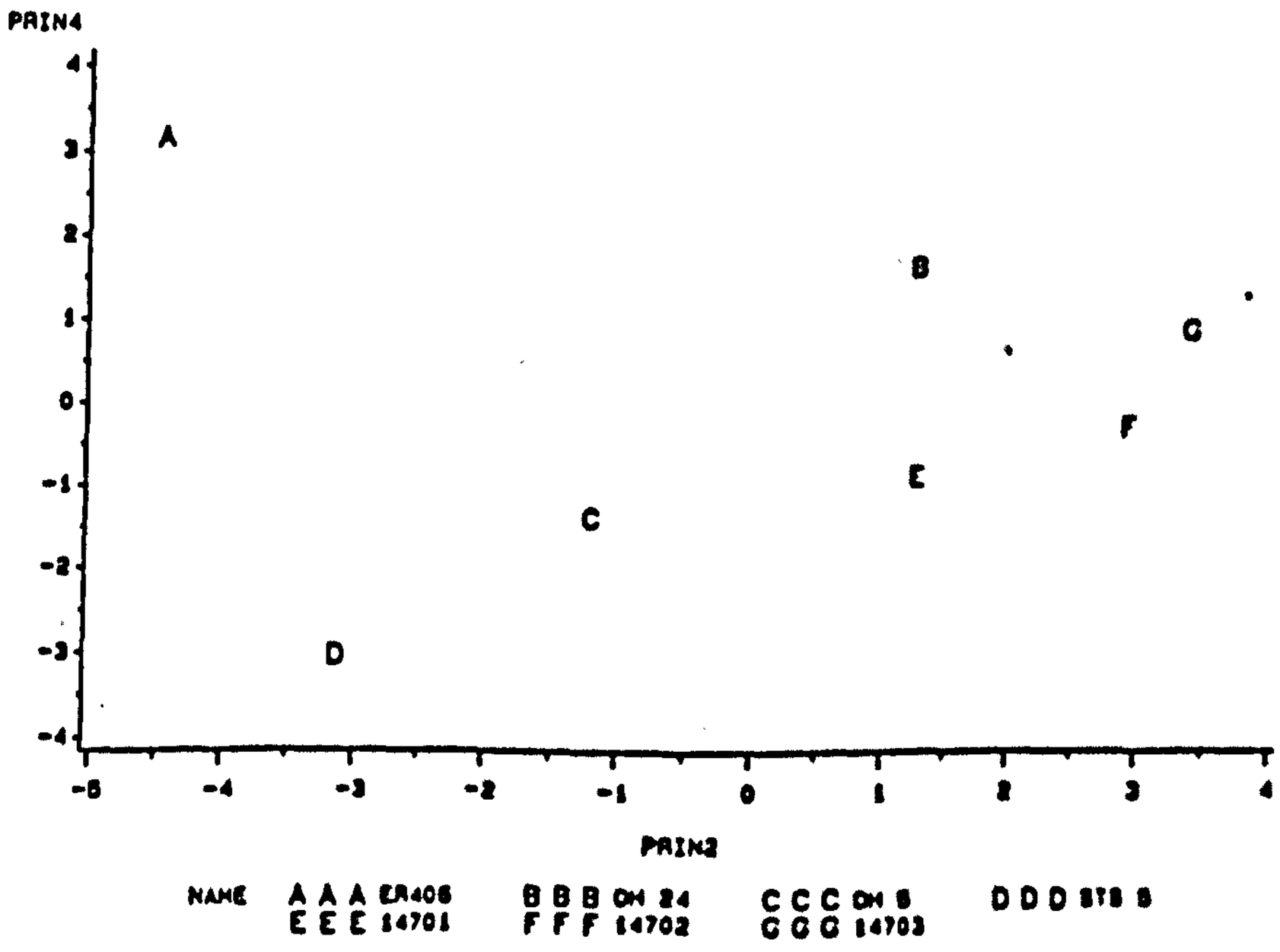



Fig B.17

FIGURE B.18 – Principal Components Analysis of 34 linear and angular dimensions adjusted for the square root of the midline area

a)




b)

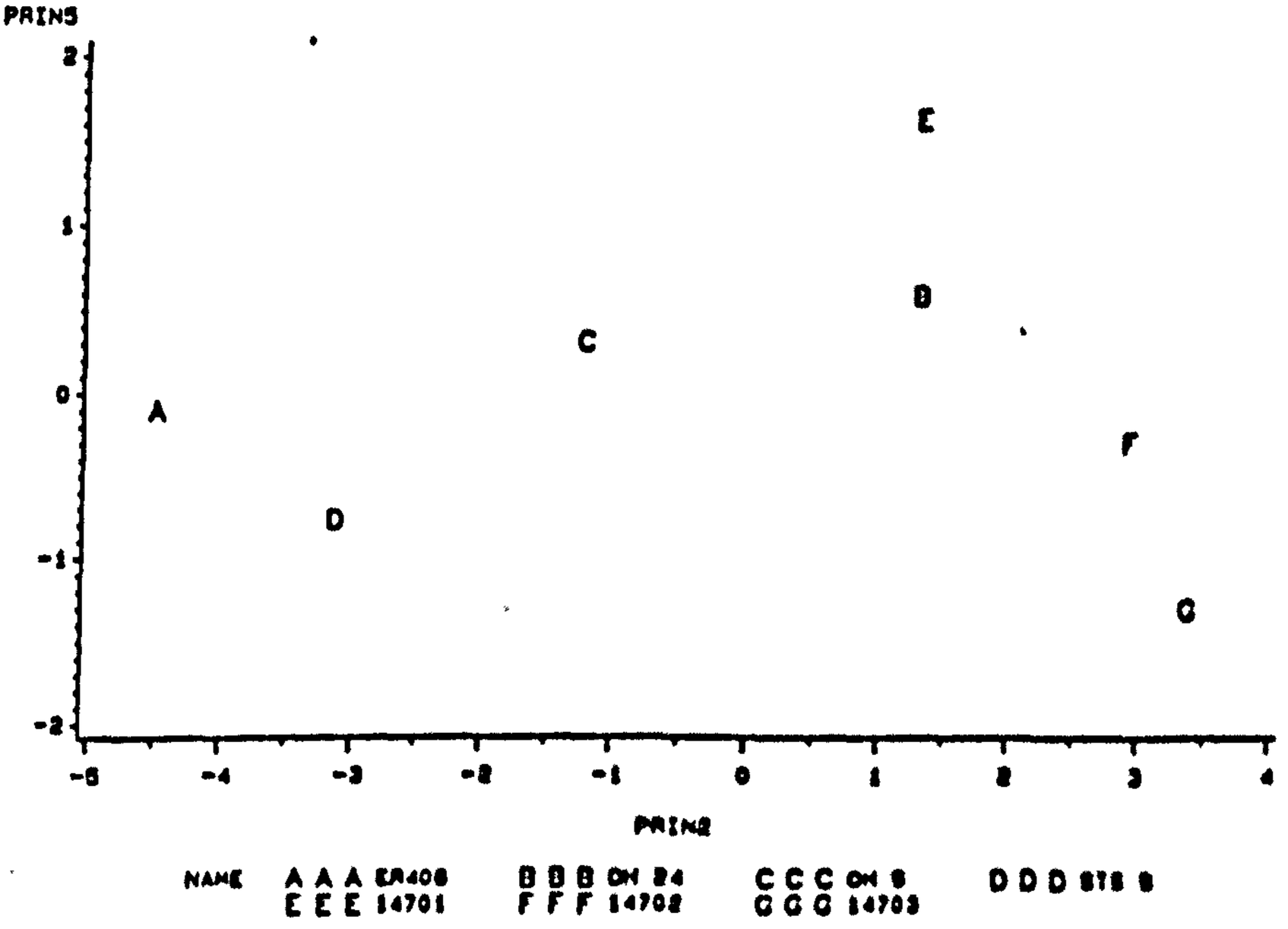



Fig B.18

## II. Canonical Analyses

The PCAs and the Euclidean distance matrix discussed above do not distinguish the Kabwe 1 cranium from the "classic" Neanderthals. They also suggest that the Skhul V cranium is within the extreme limits of morphological variation of this group, tending towards the a.m. fossils. Since these findings disagree with those of other workers (discussed later), they were further tested by two canonical analyses. In the first the Kabwe and Skhul V crania were included in a group together with the "classic" Neanderthals, in the second they were entered separately.

The plots of the first three canonical axes from these studies are presented in figures B.19 and B.20 (these three axes account for >95% of the total between group variability in both analyses). In general there is a high degree of concordance between the analyses, suggesting that the inclusion of the Kabwe and Skhul V crania in a group together with the "classic" Neanderthals has little if any effect on the phenetic relationships of this and the other groups of crania.

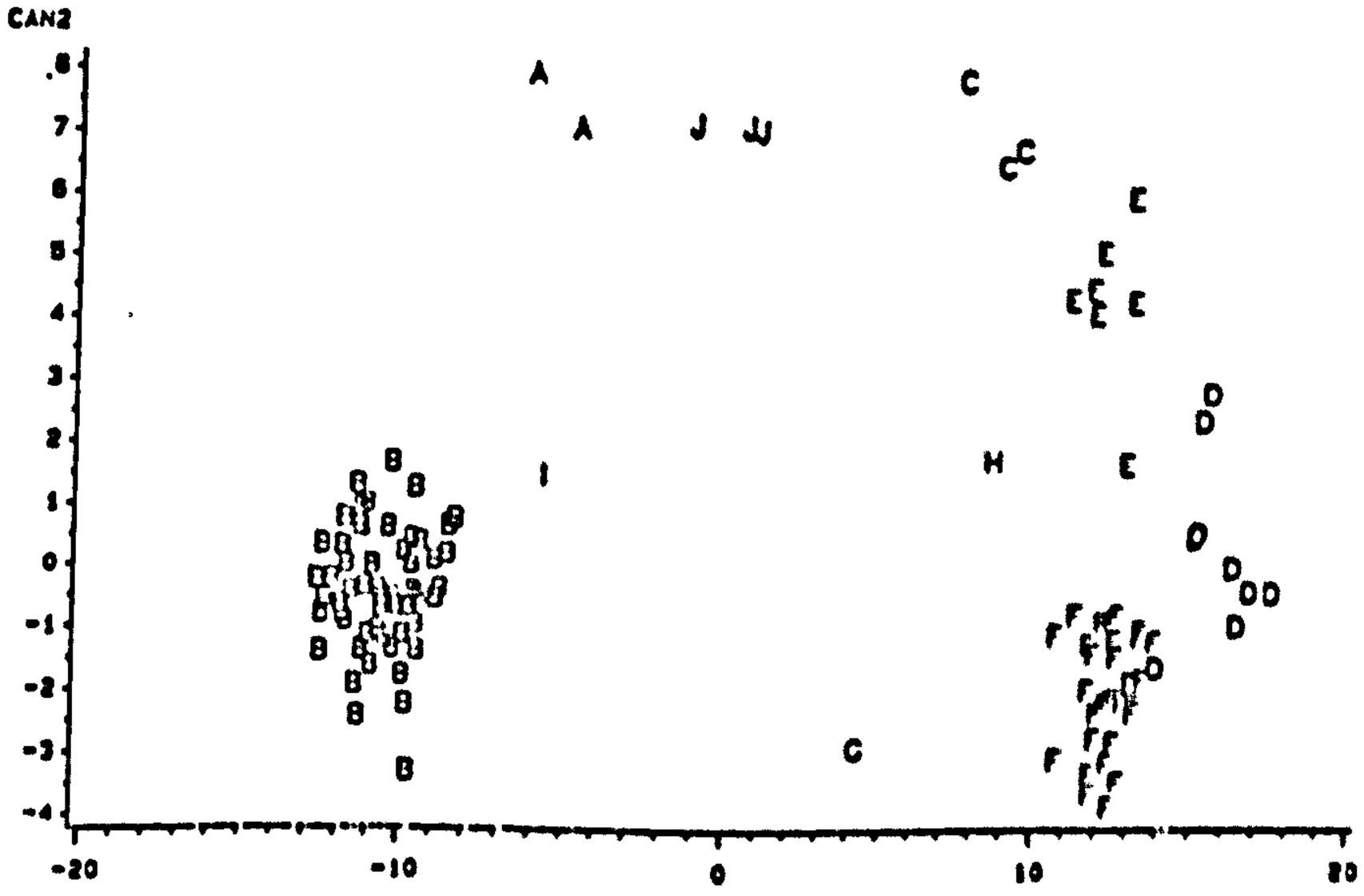
In figure B.19 the group comprising the "classic" Neanderthals and the Kabwe and Skhul V crania appears no more variable than the chimpanzees and only a little more so than the negroes. This contrasts markedly with the study in which the Kabwe and Skhul V crania were entered separately. In figure B.20 both the Skhul V on axis II and Kabwe on axis III crania are markedly separated from the "classic" Neanderthals.

The Mahalanobis' distances calculated in the course of this analysis suggest that both the Kabwe and the Skhul V crania are significantly different from the

"classic" Neanderthals and a.m. fossils (Kabwe−Neand.=10.1 SDU, P<0.01, Kabwe−a.m.=9.9 SDU, P<0.01, Skhul V−Neand.=11.05, P<0.01, Skhul V−a.m.=7.7 SDU, P<0.01).

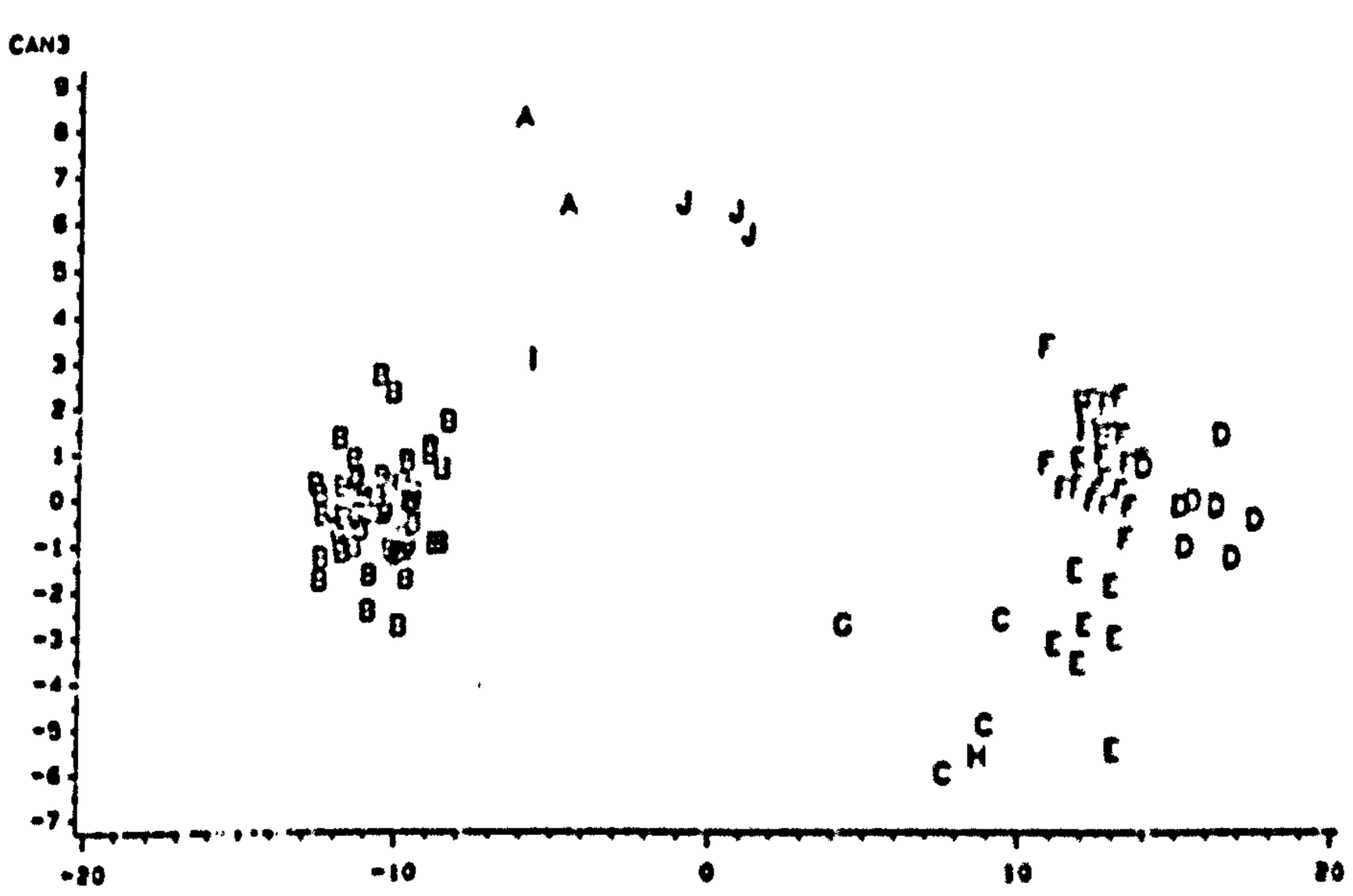
FIGURE B.19 – Canonical Analysis of 34 scaled linear and angular dimensions adjusted for the square root of midline area. The Kabwe + Skhul V crania are included in the group of Neanderthals and Neanderthal-like crania

a)




GROUP A = *A. boisei* B = *Pan* C = *H. erec.* D = a.m. *H. sap.*
E = Neand. + Kabwe1 + SkhulV F = Negro G = OH 24
H = Stein I = Sts 5 J = ER 1470

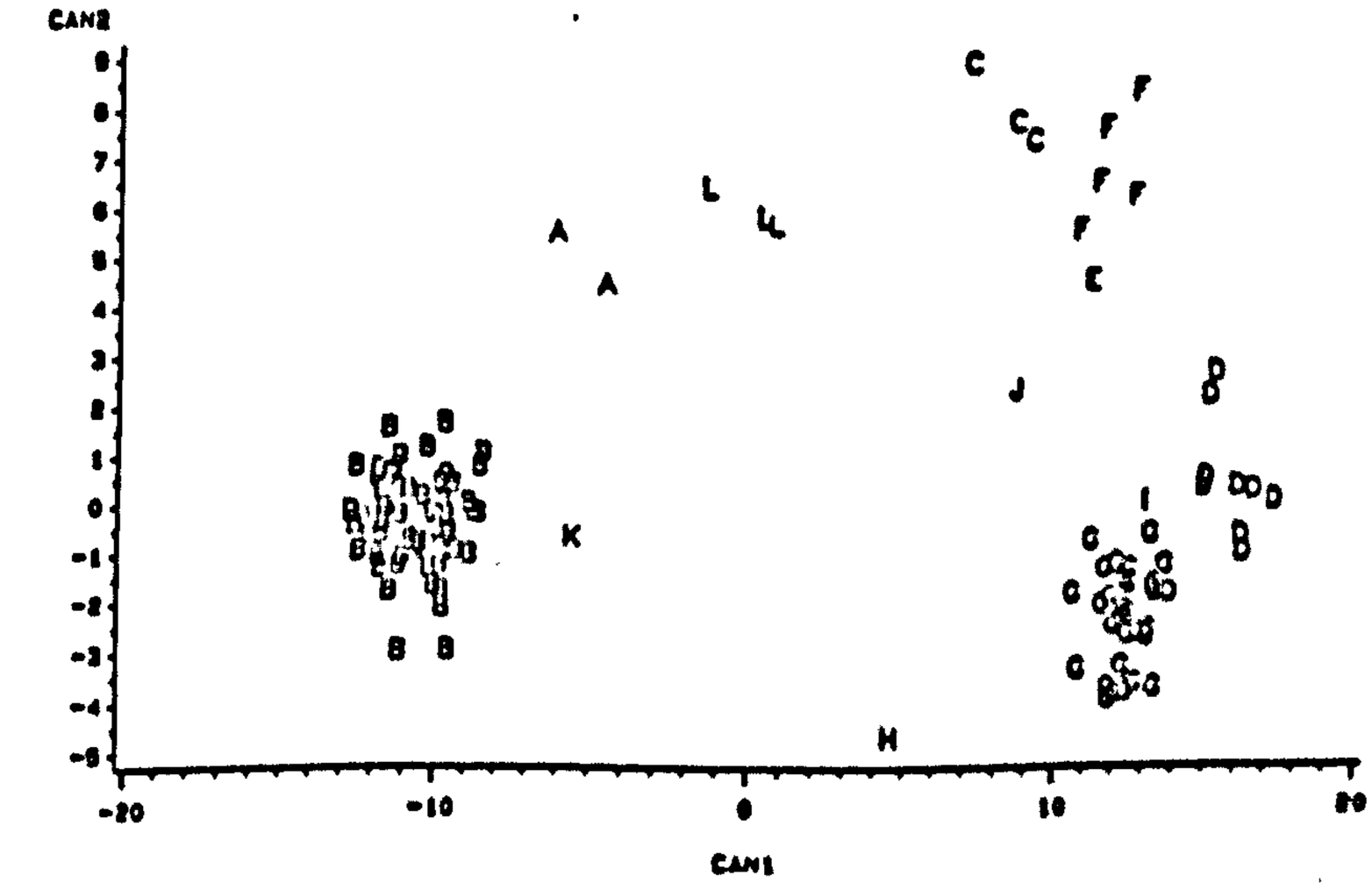
b)



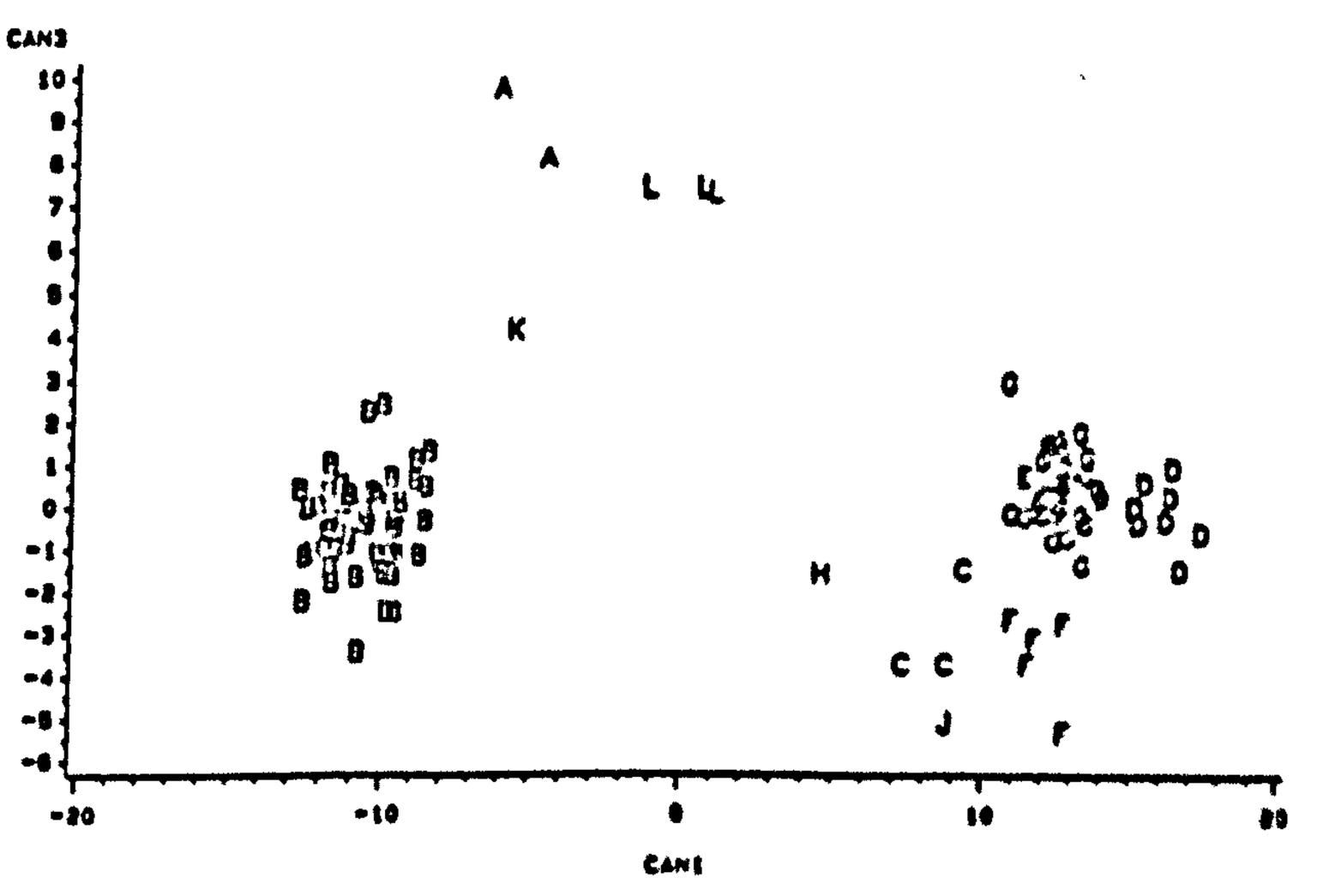

GROUP A = *A. boisei* B = *Pan* C = *H. erec.* D = a.m. *H. sap.*
E = Neand. + Kabwe1 + SkhulV F = Negro G = OH 24
H = Stein I = Sts 5 J = ER 1470

Fig. B.19

FIGURE B.20 – Canonical Analysis of 34 scaled linear and angular dimensions adjusted for the square root of midline area. the Kabwe + Skhul V crania are separate




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470




GROUP A – *A. boisei* B – *Pan* C – *H. erec.* D – a.m. *H. sap.*
E – Kabwe 1 F – Neand. G – Negro H – OH 24
I – Skhul V. J – Stein. K – Sts 5 L – ER 1470

Fig. B.20

# DISCUSSION OF RESULTS

## A. Univariate analysis

By and large the univariate analyses have been of little use in determining phenetic groups. In general apes contrast with men in a number of dimensions. Certain fossils consistently appear like the modern humans, including all of the fossil crania of anatomically modern *Homo sapiens*, the "classic" Neanderthals, Skhul V, Kabwe 1, and the Steinheim cranium. The specimens attributable to the grade of *Homo erectus* are generally more like the modern humans than the apes but there is evidence of a high degree of variability within this grouping. The specimens of early *Homo* (KNM–ER 1470, OH 24) and of *Australopithecus* also appear to be variable in morphology.

Considering the problems of character correlation and of adequately summarising the information contained in the charts of appendix C it is my intention to concentrate on a summary and discussion of the results of the multivariate study.

## B. Multivariate analysis

The principal aim of this series of multivariate analyses has been to identify clusterings of fossil crania which appear distinct from other crania and which are not unduly variable. The studies have also allowed the examination of patterns of within–group variability.

## C. The identification of phenetic groups

The PCAs of raw data (figs B.1–9) allow the identification of a number of discontinuities in the variation of cranial form in fossil hominids which suggest the following groupings:

a) Archaic and anatomically modern (a.m.) *Homo sapiens*

b) The crania attributed to *Homo erectus*

c) The crania of *A. boisei*

d) Isolated crania (KNM–ER 1470, OH 24, Sts 5, and Steinheim)

Principal component I represents a major component of this separation and scores on it appear to be related to size differences between the crania (they are significantly correlated with the square root of cranial midline area – table B.1, $r = 0.96$, $P < 0.001$).

The study of scaled data (fig. B.10) produces similar results. Once again the correlation of the scores of crania on PCI with their "size" is large and significant (table B.2, $r = -0.70$, $P < 0.001$). This suggests that scores on PCI should not be interpreted as reflecting simple size effects, rather they reflect complex shape differences associated with (but not necessarily entirely consequent upon) cranial vault expansion. Reasonable confidence can therefore be attached to the assertion that these preliminary phenetic groupings are not purely determined on the basis of size differences but that shape differences also intrude.

The preliminary phenetic groupings were studied by further PCAs and by canonical analyses:

a) Archaic and recent *Homo sapiens*

*Anatomically modern Homo sapiens*

It has been noted earlier that the PCAs using both raw and scaled data from the group of fossil a.m. humans have demonstrated differences between the European crania and those from different regions.

Within the European crania Predmost 3 is most like Skhul V (figs. B.2, B.11) and the "classic" Neanderthals. Smith (1984) has noted that this cranium is clearly modern in morphology but that the face and supraciliary ridges are robust, the vault and forehead is relatively low and there is a well-developed occipital hemi-bun. He uses these features, which he has noted in other fossil a.m. central European material, to suggest a degree of morphological continuity between the preceding Neanderthal populations and fossil a.m. humans. This he takes to imply continuity in the gene pool. The impression of some degree of similarity between the robust Predmost 3 cranium and Neanderthals is supported by the current analyses.

The other central European fossils (Mladec 1 and Brno 3), are placed more centrally within the fossil a.m. sample in the PCAs (figs. B.2-B.5, B.11-B.14) though the Euclidean distance matrix indicates that the nearest neighbour to Predmost 3 is Mladec 1 and to Mladec 1 is Brno 3. Smith (1984) considers Mladec 1 and Frayer (1984) considers Brno 3 to be female. The differences

between the female and the male central European crania may be the result of the large degree of sexual dimorphism noted within Upper Palaeolithic crania by Frayer (1984) though Brno 3 is further from Mladec 1 (29.8 units) than is Mladec 1 from Predmost 3 (26.5 units). The evidence for morphological continuity between this population and Neanderthals is no greater than that for continuity between western Europeans and Neanderthals (see figs. B.2 and B.11). Stringer *et al.* (1984) in reviewing the western European record did "not recognise any fossil specimens with an intermediate morphology between Neanderthal and modern types".

On the one hand Smith, (1984) sees continuity between central European fossil a.m. *Homo sapiens* and Neanderthals while on the other, Stringer *et al.* (1984) see discontinuity between western Europeans and Neanderthals. The evidence of this study is that the central and western European fossil a.m. material is very similar and that such a contrast in opinion is unjustified.

It may be argued that the current study suffers from inadequate data to adequately describe the differences in cranial morphology between "classic" Neanderthals and fossil a.m. humans and may therefore fail to properly describe intermediacy. Against this it can be said that a morphological discontinuity between these fossils could be identified from studies based on scaled data (fig. B.11) and less clearly from raw data (fig. B.2).

Wolpoff *et al.* (1984) have considered the morphological relationships of the Wadjak 1 cranium. They indicate a number of features in which it is reminiscent of both australoid and southern Chinese crania and point to a number of

dissimilarities between it and the Keilor 1 cranium (*contra* Weidenreich, 1945). This study has clearly demonstrated the distinctive morphology of both crania (figs. B.4, B.5, B.13, B.14). Wadjak 1 is separated from all other fossil a.m. crania on PCII and Keilor on PCIV in the analyses of both raw and scaled data.

The two crania from Africa, Fish Hoek 1 and Gamble's Cave 4 are distinct from all other fossil a.m. crania on PCs III and V respectively from the PCAs based on both scaled and raw data (figs. B.4b, B.5b, B.13b, B.14b). Furthermore they appear quite different from each other in these analyses. This is consistent with their different attributions (Fish Hoek – Bushman, Keith, 1931, Gamble's cave – Nilotic Negro, Rightmire, 1975).

*Neanderthal and Neanderthal–like crania*

In the PCAs of raw data the "classic" Neanderthal group overlaps the group of fossil anatomically modern crania (figs. B.1, B.2, B.3). It is clear from the studies of scaled data (figs. B.10, B.11, B.12) that this overlap reflects size influences because, using scaled data, there is a clear discontinuity between the "classic" Neanderthals and anatomically modern forms. To the positive extreme of PCI are the "classic" Neanderthals and the Kabwe 1 cranium and to the negative extreme are the anatomically modern crania.

The representatives of archaic and modern forms of *Homo sapiens* are arranged as two overlapping spheroidal distributions (fig. B.11a). The region of overlap is occupied by the Steinheim cranium, Skhul V and Predmost 3 in the

studies of scaled data (fig B.11). The studies of raw data, however, separate the Steinheim cranium from the representatives of archaic and fossil a.m. *Homo sapiens* (figs B.1–2).

Had the Steinheim, Skhul V and Kabwe crania not been included in this study there would have been little difficulty in demonstrating a phenetic group of anatomically modern *Homo sapiens* and a distinctive group of "classic" western European Neanderthals. The inclusion of these crania has, however, led to some difficulties in identifying discontinuities. The Steinheim and Skhul V crania appear intermediate in morphology between fossil a.m. *Homo sapiens* and the "classic" Neanderthals whilst the Kabwe cranium is not differentiated from the "classic" Neanderthals by the PCAs or the Euclidean Distance matrix (table B.3). It is worthwhile re–examining the metrical findings of previous workers in relation to the affinities of these fossils.

The degree of similarity between the Kabwe cranium and the "classic" Neanderthals of Europe has been considered by several authors (e.g. Woodward, 1921, Morant, 1928, Singer, 1954). Morant (1928) whilst demonstrating metrical differences considered it more similar to the Neanderthals than to modern humans. From a comparison of individual measurements he concluded that the "Neanderthaloid type is rather less widely removed from modern man than the Rhodesian" (=Kabwe 1) (but a generalised coefficient suggested the reverse).

Stringer (1974a) in his multivariate study of the cranial morphology of later Pleistocene hominids presents $D^2$ matrices based upon analyses of regional and more anatomically comprehensive data. His study, based upon 25 variables from

a wide anatomical distribution, shows that the nearest neighbour to the centroid of his cluster of "classic" European Neanderthals is the Kabwe 1 cranium. The distance suggests a difference which is significant at the 1% level. The Steinheim cranium and Skhul V are further from the "classic" Neanderthal centroid and are also significantly different. All three crania are statistically significantly distant from the centroid of crania from the Upper Paleolithic.

Howells (1970) has examined the relationship of Skhul V to modern human and "classic" Neanderthal crania. He does not present a matrix of distances but his plots of discriminant functions indicate that the morphology of Skhul V is broadly intermediate between modern and Neanderthal crania.

Van Vark (1984) concluded that the Steinheim and Kabwe 1 crania ,"while being mutually relatively close, are very distinct from all other skulls". He presents a distance ($D^2$) matrix in which Steinheim and Kabwe 1 are separated by 13 SDU (N.S.) whilst both are about 40 SDU ($P<0.05$) from the "classic" Neanderthal centroid. In studies where all fossils were entered as individuals the nearest neighbours to Skhul V are recent and Upper Paleolithic humans ($D^2=6.7-40$ SDU) followed by "classic" European Neanderthals ($D^2=19-55$ SDU).

Consistently these studies have shown that the Kabwe 1, Skhul V and the Steinheim crania are different from the crania of the "classic" Neanderthals, a finding which contrasts with those of the PCAs presented above.

The canonical analyses considered earlier also conflict. The study which included the Kabwe and Skhul V crania in a single group together with the

"classic" Neanderthals did not suggest any increased within-group variability relative to the modern groups. This contrasts with the large and significant Mahalanobis' distances calculated between the Kabwe and Skhul V crania and the centroids of the "classic" Neanderthals and fossil a.m. humans when they were entered separately into a canonical analysis (fig. B.20). This canonical analysis resulted in a pattern of dispositions of the Kabwe, Skhul V, Neanderthal and fossil a.m. crania which agrees with that found by Howells (1970) and Stringer (1974a) (Incidentally, the stepwise removal of "classic" Neanderthals from their group in a series of unreported canonical analyses failed to show any significant difference between each and the remainder).

These findings are problematical. The PCAs and Euclidean distance matrix suggest that the Kabwe cranium and to a lesser extent Skhul V are indistinguishable (using these data) from the "classic" Neanderthals whilst canonical analysis suggests the reverse. The reasons for this are unclear but it may be a result of the fact that canonical analysis is a discriminant technique and, as such, variables are given different weightings in accordance with their utility in distinguishing groups (Mardia, pers. comm.).

It is clear from the canonical analysis that the Kabwe 1 and Skhul V crania are distinct from the "classic" Neanderthals and fossil a.m. humans. The fact that this was not confirmed by preliminary PCAs or from an examination of the Euclidean distance matrix illustrates a potential weakness in numerical phenetic studies. The hypotheses that Kabwe 1 and Skhul V have distinct morphologies were tested only because of prior work by others. In isolation, the preliminary

multivariate studies would have been misleading.

b) *Homo erectus*

The crania representing the grade of *Homo erectus* are clearly identifiable in figure B.1 as an apparently homogenous group. The study of scaled data (fig. B.10) does, however, suggest a high degree of morphological variability (though only 1.5–2 times that within fossil a.m. *Homo sapiens*). This implies that though their sizes are similar they differ in morphology. This view is consistent with the findings of Stringer (1984), Wood (1984) and Bilsborough and Wood (1986) but disagrees with the assessment of Rightmire (1984a).

It should be noted that each of the representatives of *Homo erectus* included in this study has been heavily reconstructed (see appendix A) and may well be inaccurate. With this in mind I have included the representatives of *Homo erectus* in a group for canonical analyses in order to allow an assessment of their overall affinities.

c) Australopithecines and early *Homo*

The PCAs of this restricted collection of late Pliocene and early Pleistocene fossils are presented in figures B.8, B.9 (raw data), B.17 and B.18 (scaled data). In both studies PCI separates the gracile crania (OH 24 and Sts 5) from those which are more robustly constructed in the facial region (*A. boisei* and KNM–ER 1470, Bilsborough and Wood, 1988). There is a high correlation of the scores of crania on PCI with the square roots of the areas of their midline projections

in both studies (scaled and raw data). This may well primarily reflect the differences in facial rather than neurocranial proportions.

A clear grouping of the two crania of *A. boisei* is evident from the studies of both raw and scaled data (figs. B.1, B.10) in which they appear distinct from Sts 5, a representative of *A. africanus*. This finding is consistent with the consensus view (e.g. Howell, 1978, Grine, 1981).

The studies consistently point to a distinction between each of OH 24, Sts 5 and KNM-ER 1470 and the remaining crania though KNM-ER 1470 appears most similar to *A. boisei*. The large difference in morphology between the representatives of early *Homo*, OH 24 and KNM-ER 1470, is consistent with the findings of Chamberlain and Wood (1987).

As a result of the PCAs I have included the two representatives of *A. boisei* as a group in the canonical analyses of chapter 4 and have entered each of OH 24, Sts 5 and KNM-ER 1470 separately.

## CONCLUSIONS AND SUMMARY OF PHENETIC GROUPS

The preceding discussion has indicated the following subdivision of fossils:

1. Representatives of fossil a.m. *Homo sapiens*
2. Skhul V
3. "Classic" European Neanderthals
4. Kabwe 1
5. Steinheim
6. representatives of the grade *Homo erectus*
7. *A. boisei*
8. KNM–ER 1470
9. Sts 5
10. OH 24

This division of fossils largely concurs with the results of PCA and with the Euclidean distance matrix but its justification also depends on the results of preliminary canonical analyses which were undertaken because of the findings of other workers.

That these canonical analyses were necessary indicates a potential pitfall in the identification of phenetic groups of fossils. PCAs and Euclidean distance matrices treat all the data as being of equal weight. This is an inevitable consequence of the formulation of phenetic studies. It is clear from a cladistic viewpoint, however, that similarity may be the result of retained primitive characters as well as the result of shared derived characters.

The inevitable consequence of grouping by all types of similarity (phenetics) is that phylogenetically important differences may be swamped by phylogenetically less important similarities. The canonical analyses, by their nature, emphasise differences between groups by giving characters unequal weightings according to their discriminatory values. It is only as a result of the canonical analyses, undertaken because of the findings of previous workers, that significant differences between Kabwe 1, Skhul V and the "classic" Neanderthals were identified.

Despite the difficulties encountered in the identification of fossil groups (especially in determining the limits of variation in the "classic" Neanderthals) the PCAs of restricted subsets of fossil crania have shown a high degree of concordance with the studies of previous workers. This suggests that the need to estimate data has not resulted in any major errors and that the results of the multivariate studies are generally reliable.

The preliminary multivariate studies presented in this appendix have served to ensure that the groups of fossils which are included in the studies of chapter 4 will not result in any distortions of between-group relationships which might confuse the comparison of Fourier data and linear and angular measurements.

# APPENDIX C

# UNIVARIATE BAR CHARTS

# Appendix C

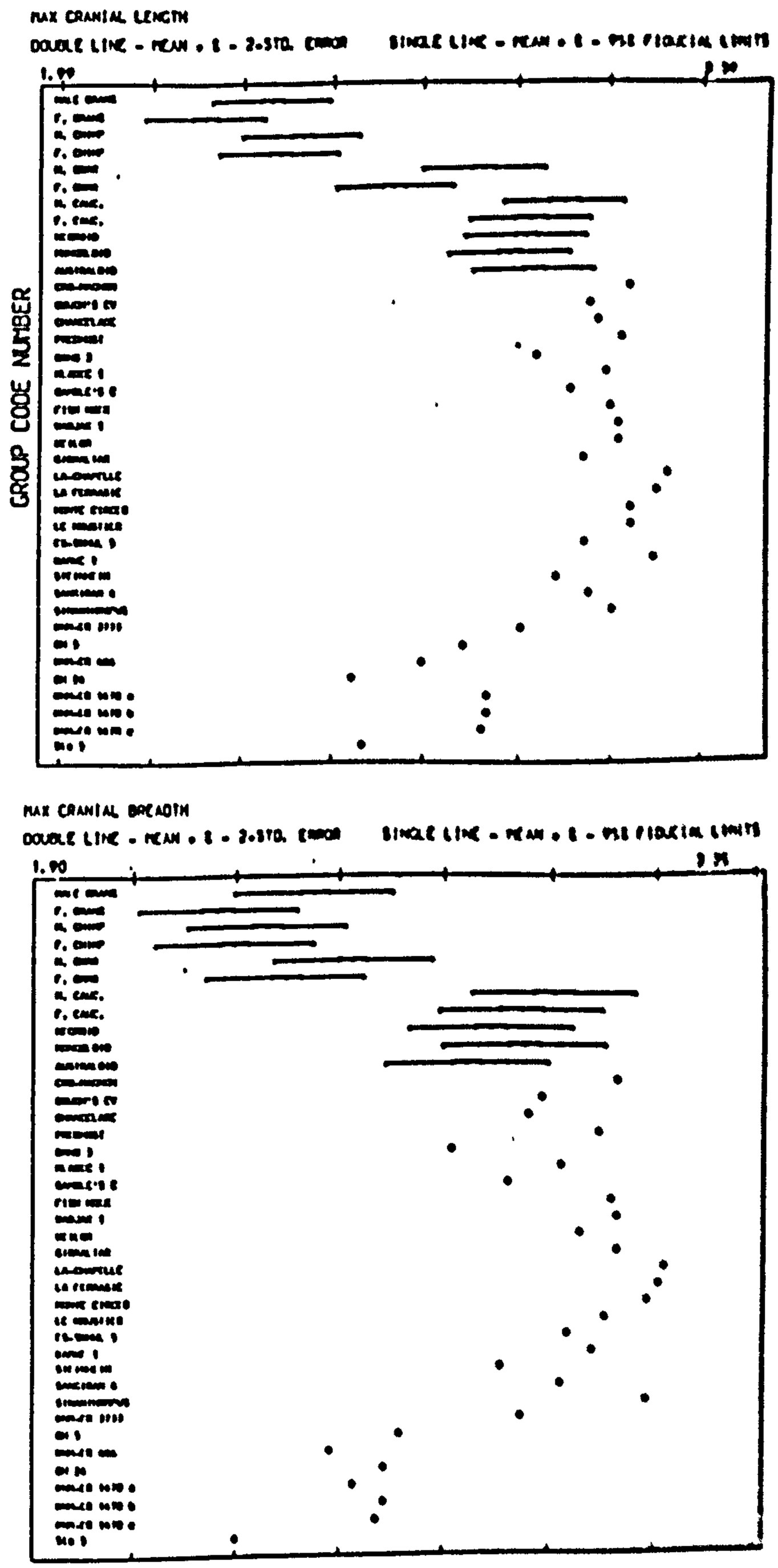



Figure C.1 – Univariate bar charts, pooled within group standard deviation, logged data.

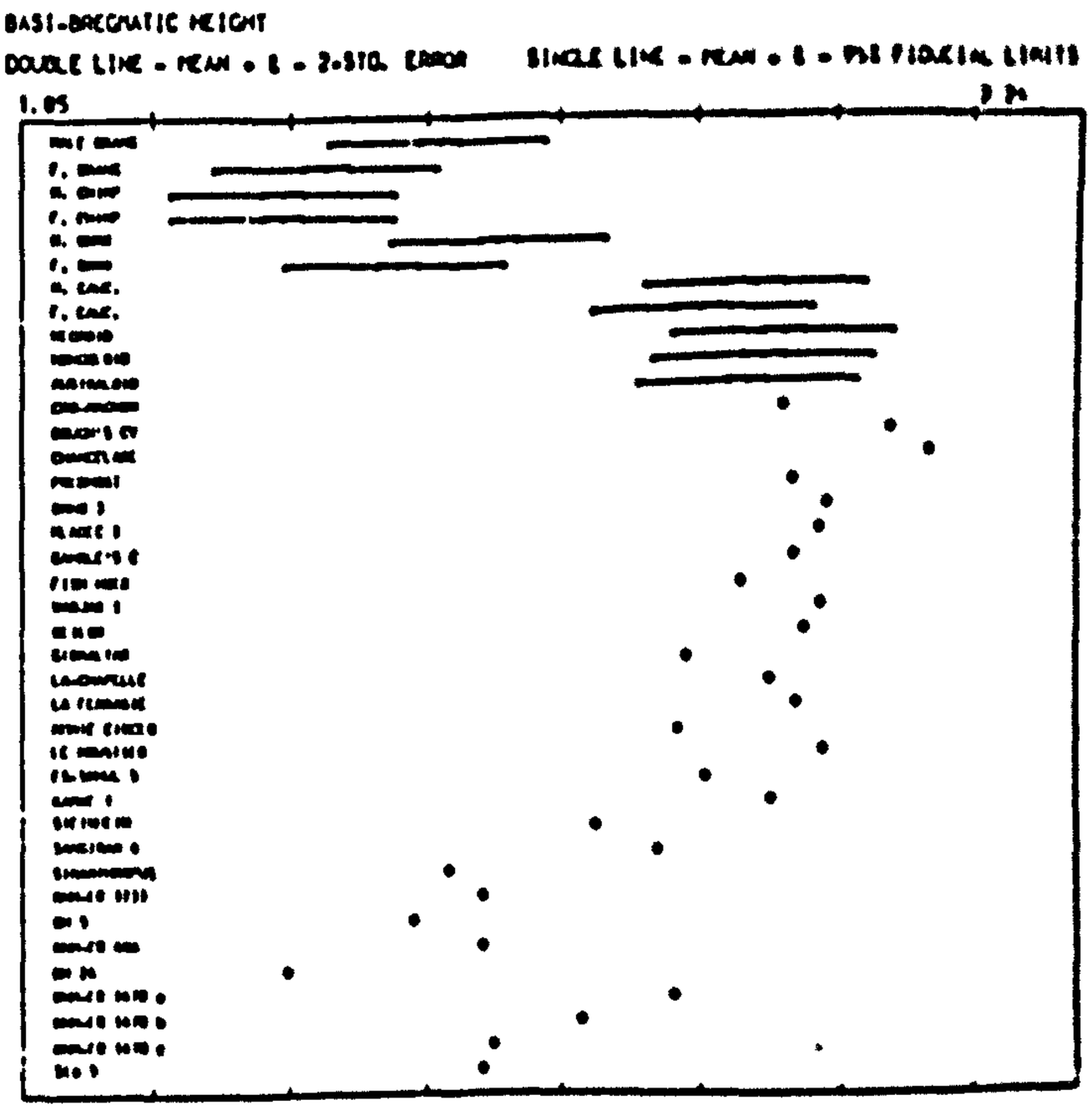
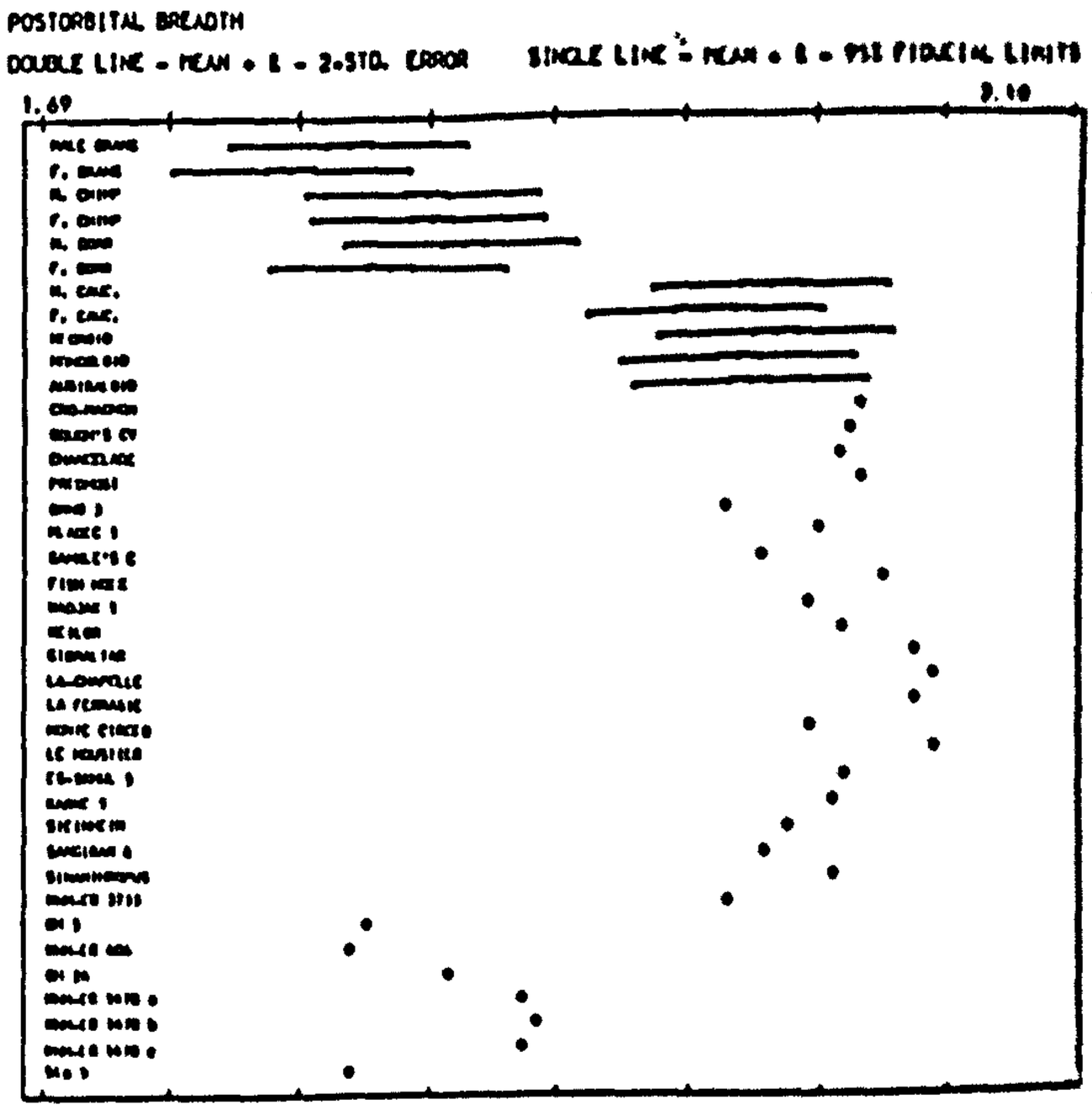
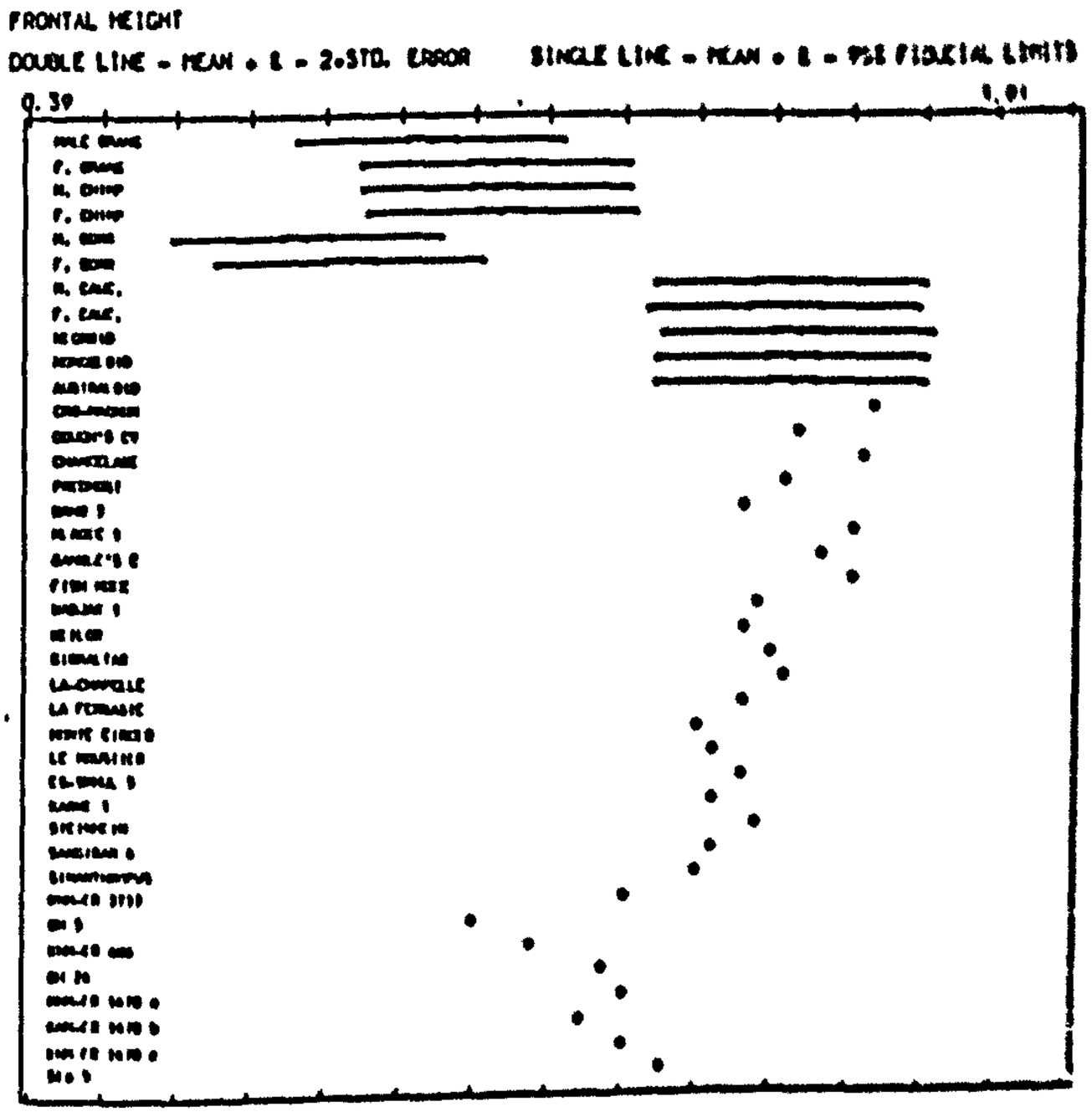



Figure C.2 – Univariate bar charts, pooled within group standard deviation, logged data.

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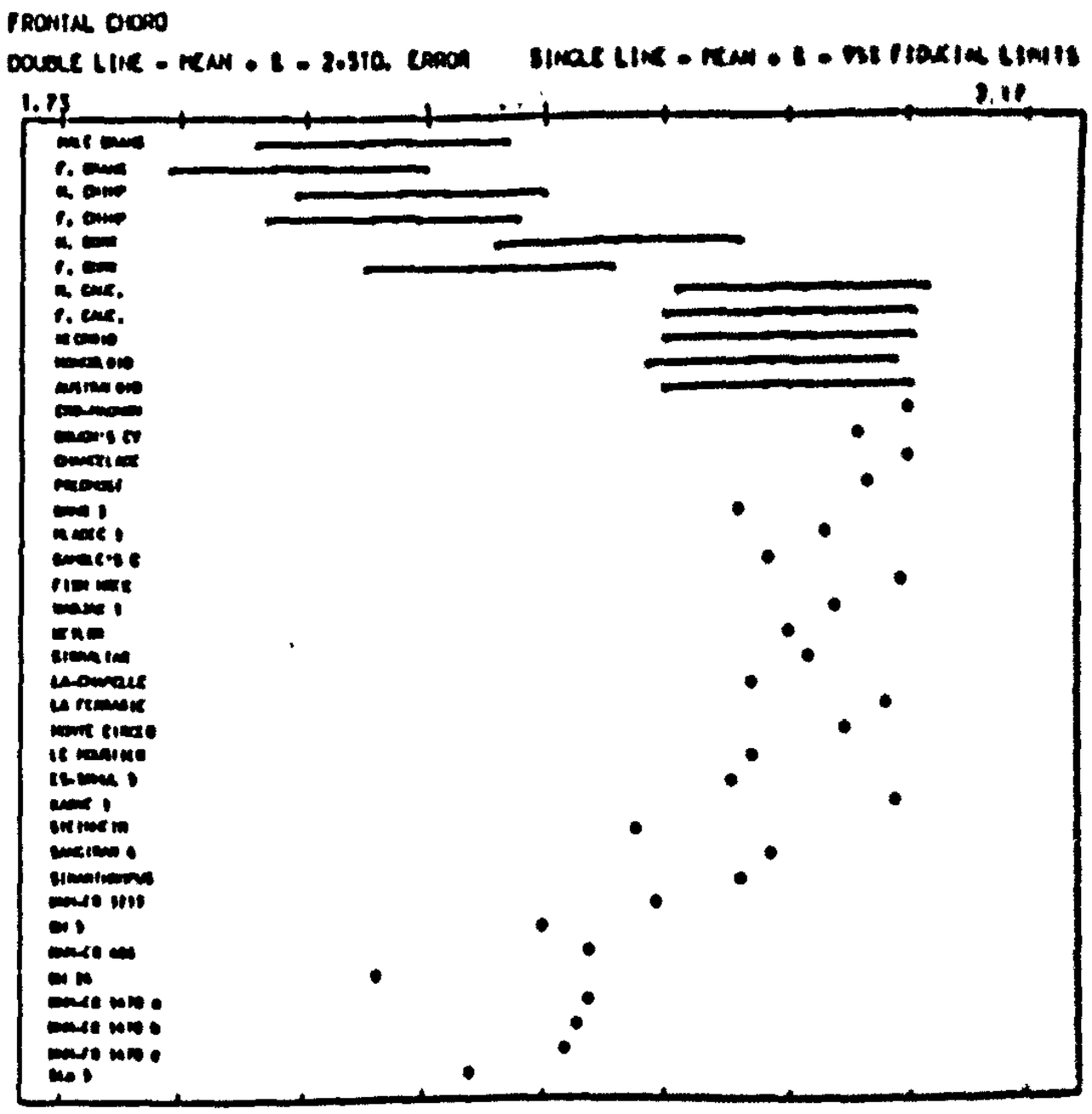


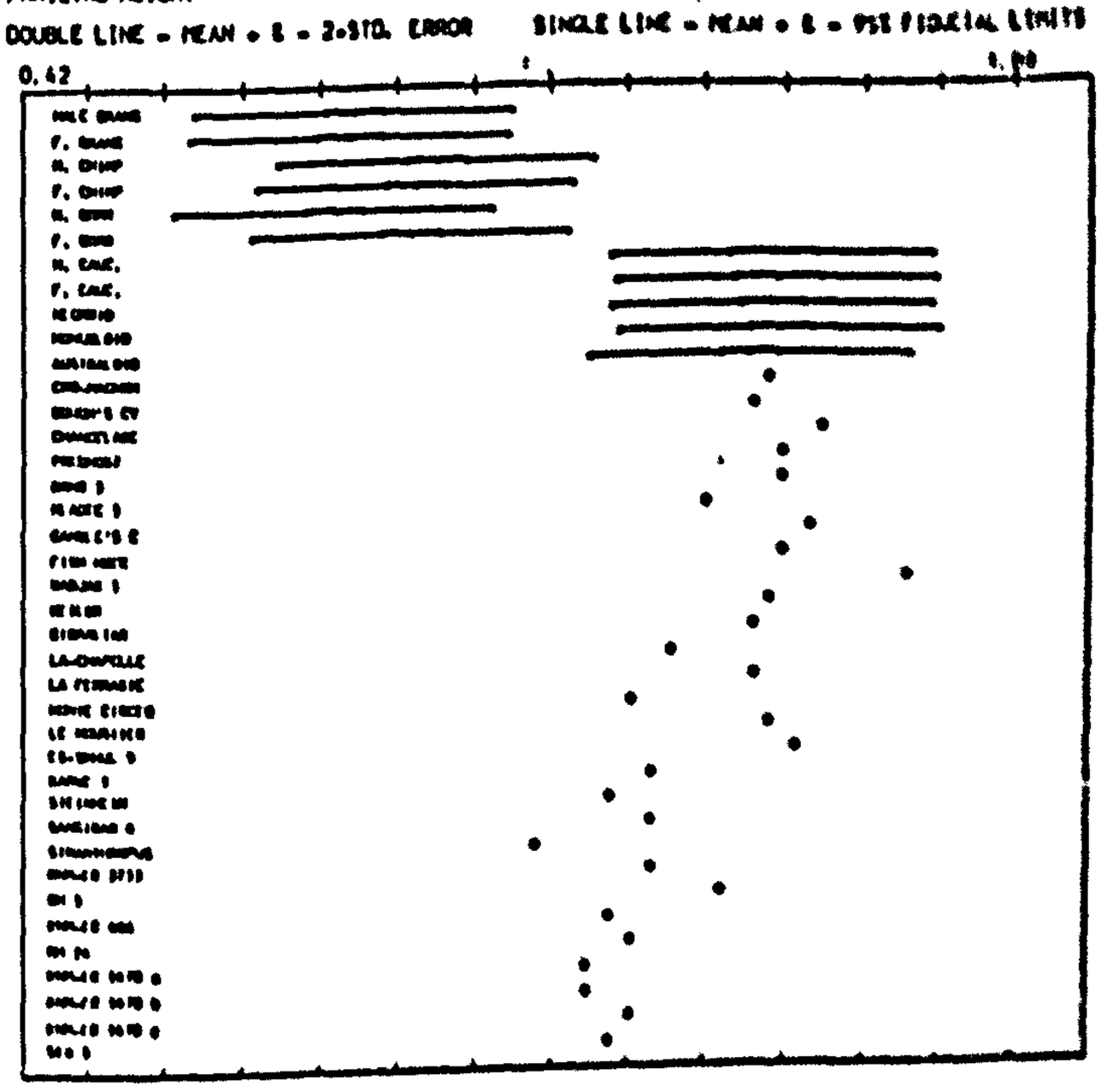




Figure C.4 – Univariate bar charts, pooled within group standard deviation, logged data.

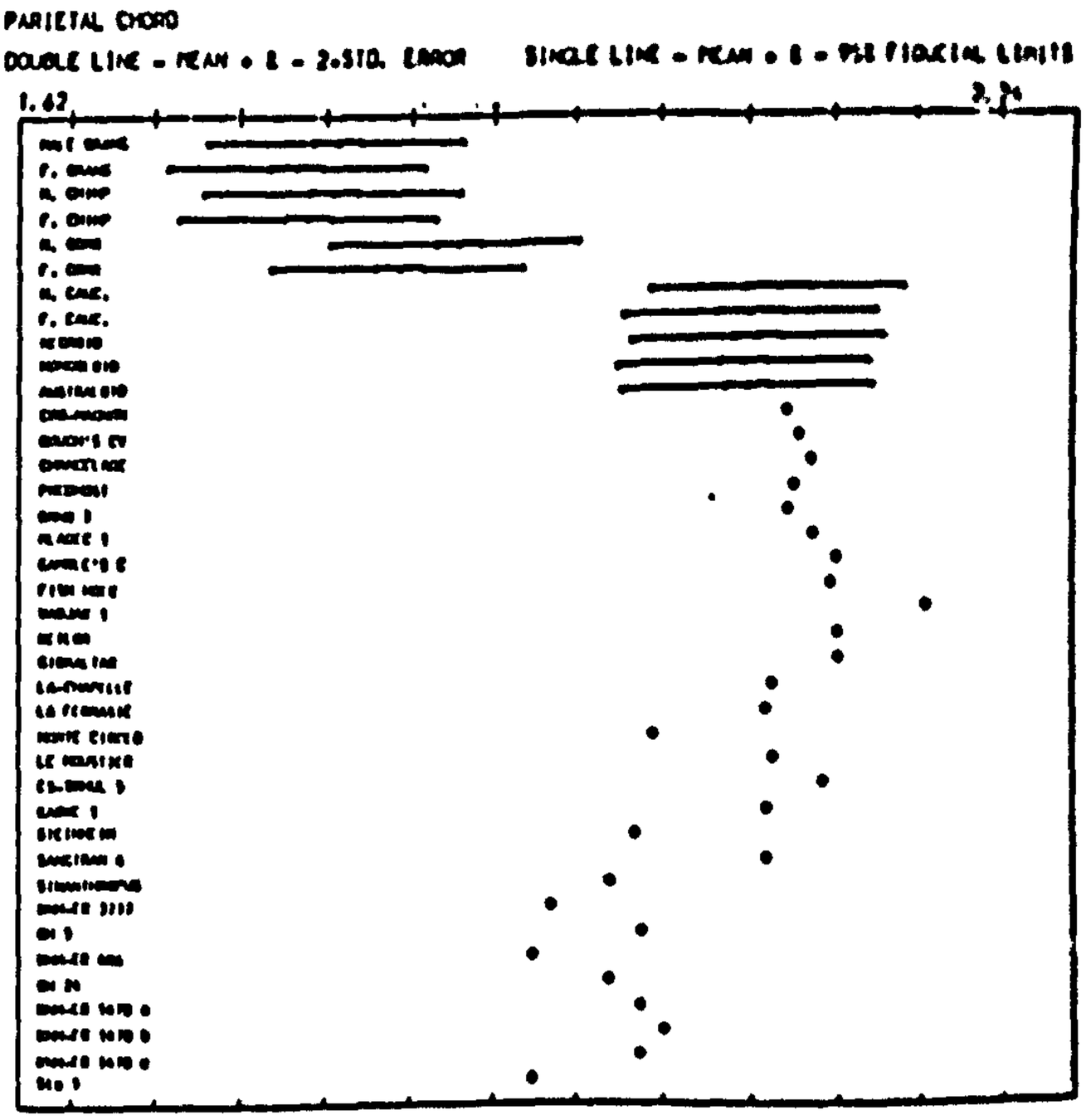
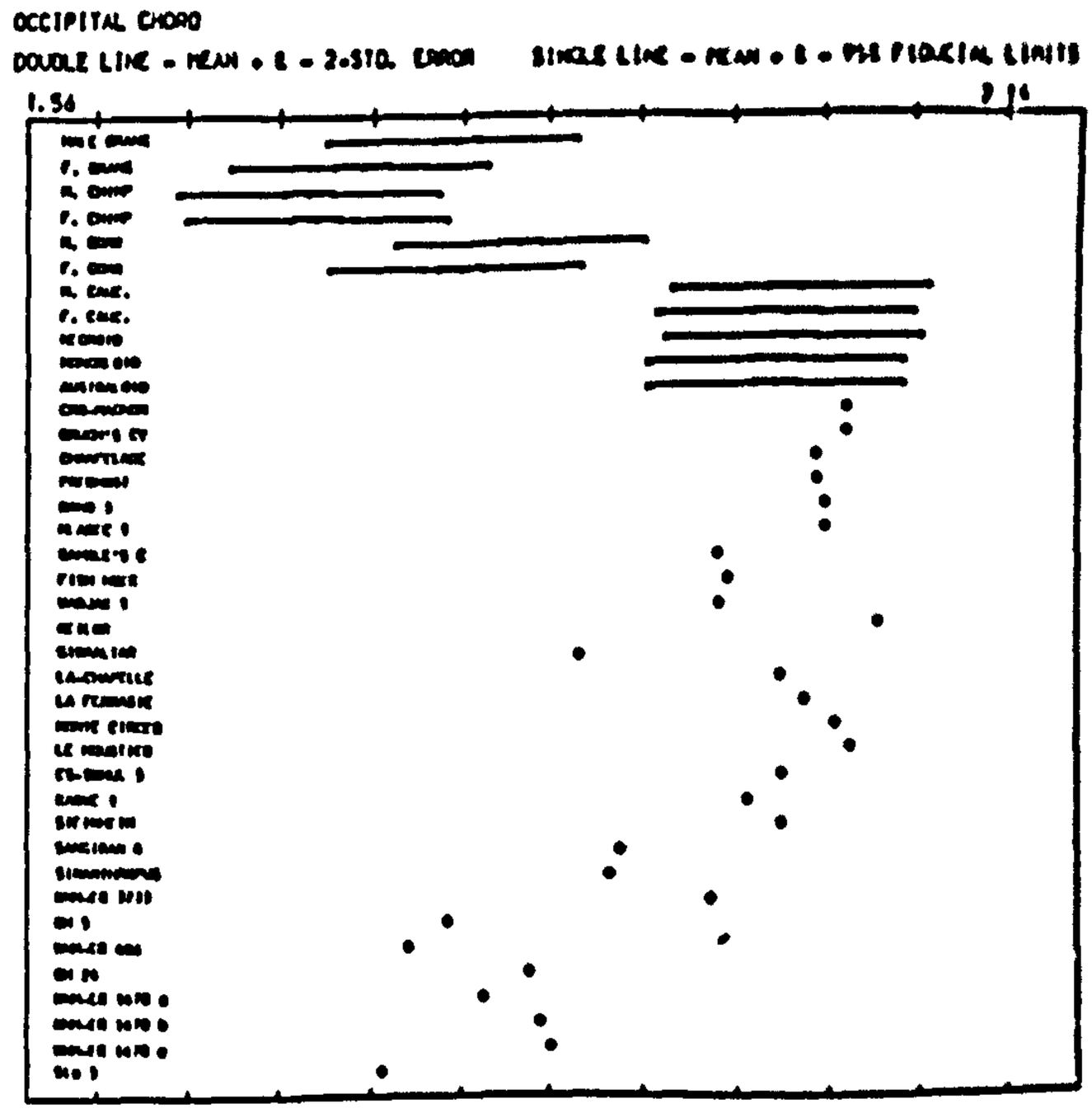



Figure C.5 – Univariate bar charts, pooled within group standard deviation, logged data.



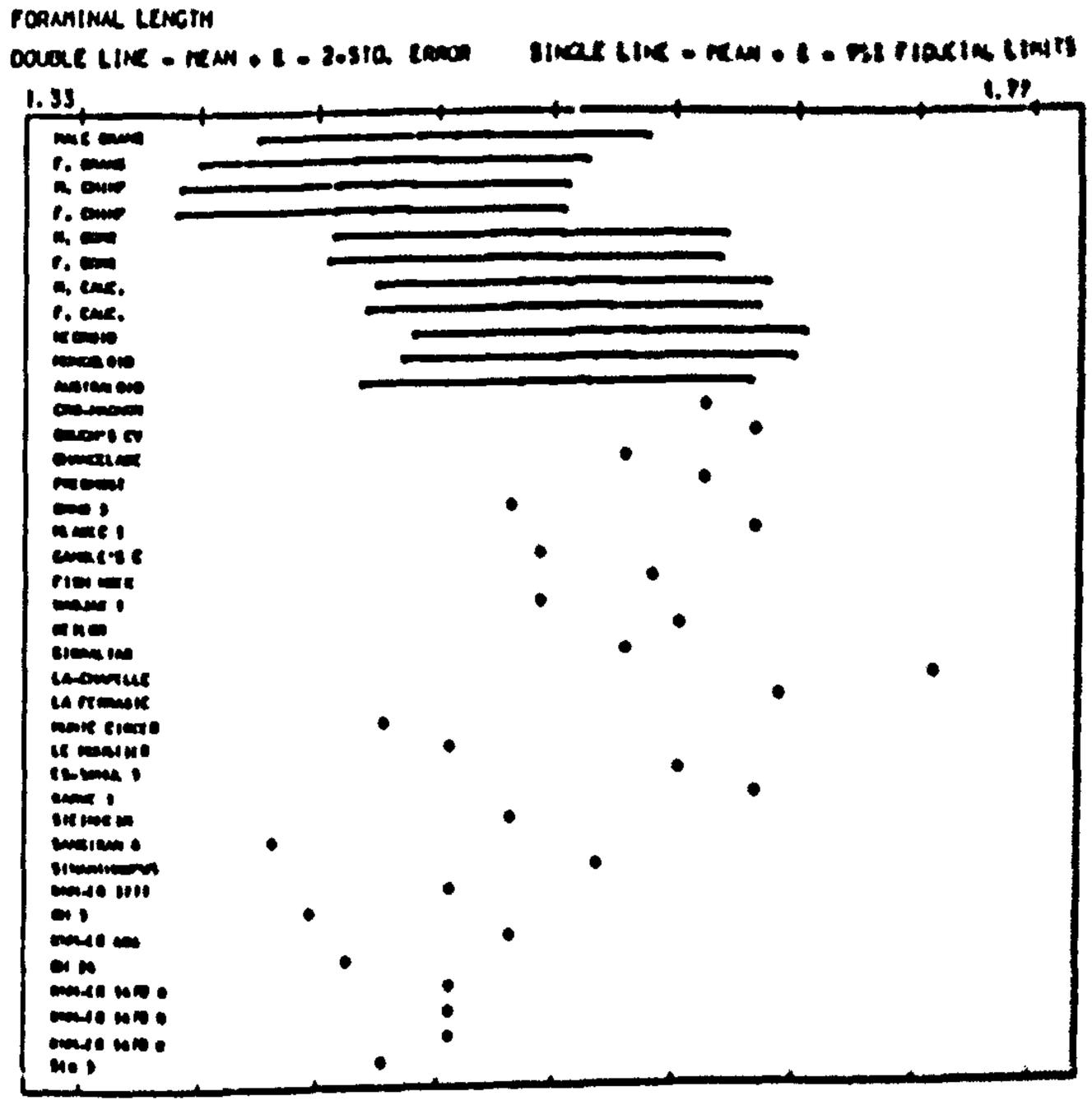
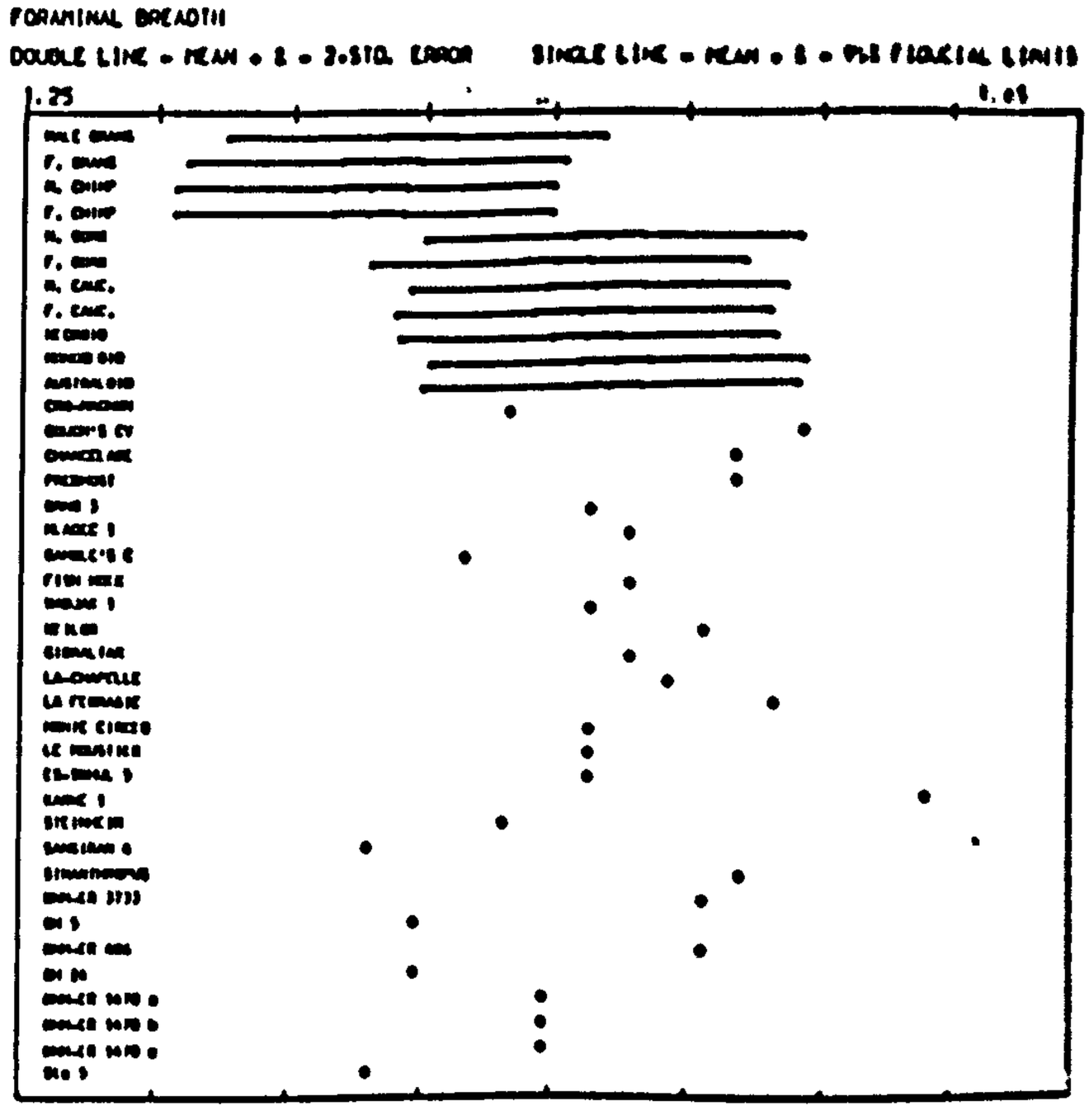




Figure C.6 – Univariate bar charts, pooled within group standard deviation, logged data.



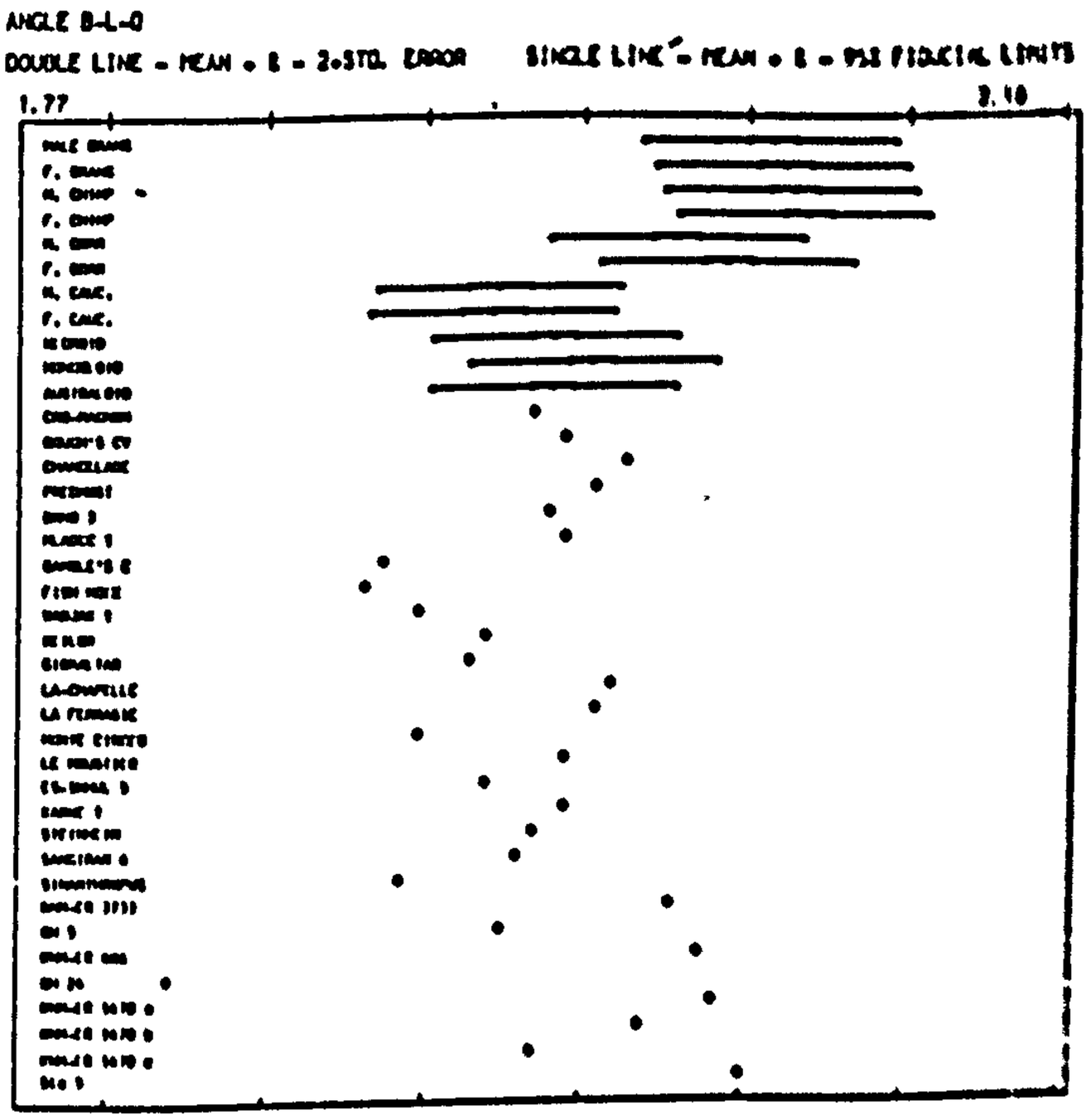
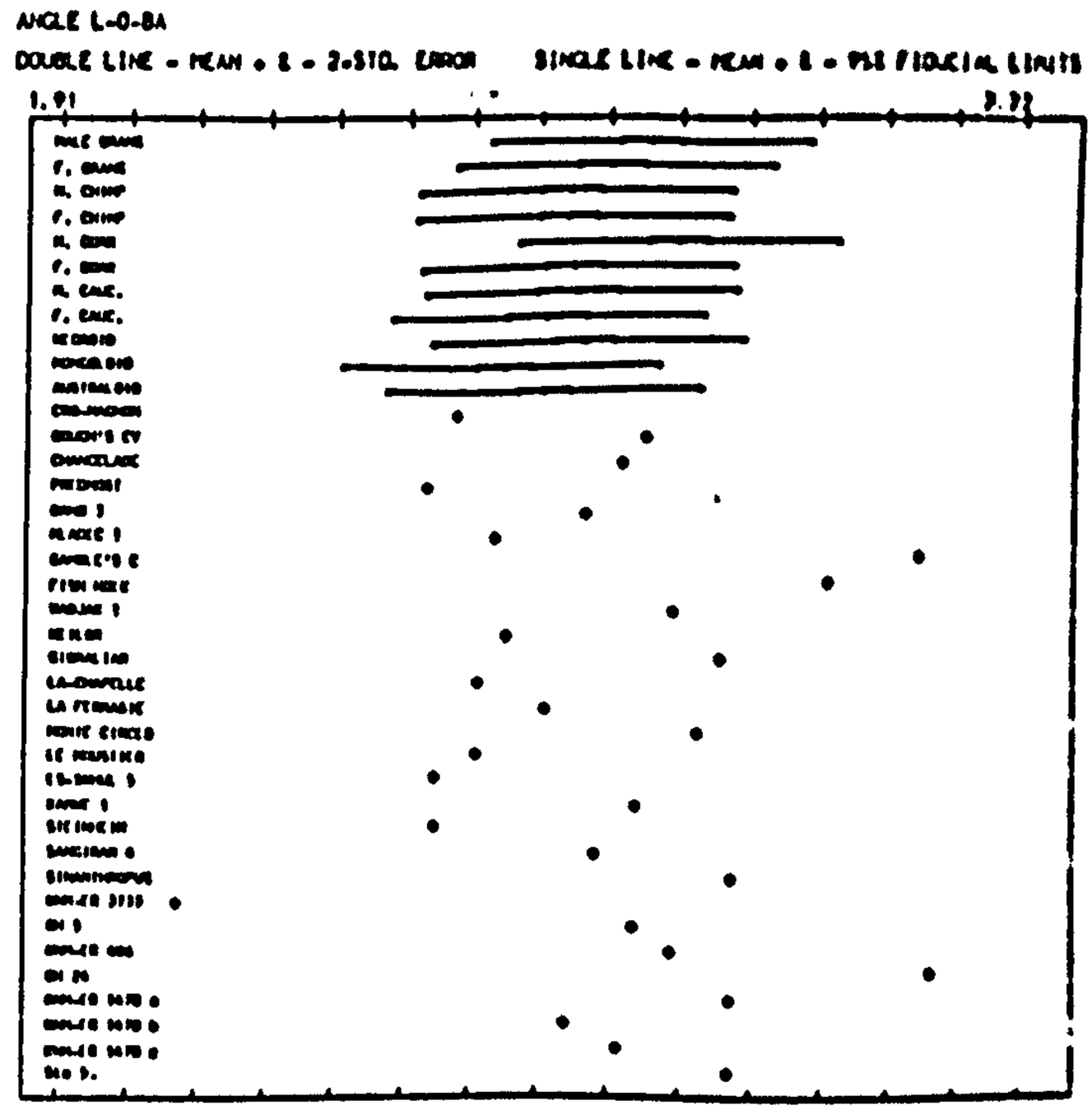




Figure C.7 – Univariate bar charts, pooled within group standard deviation, logged data.



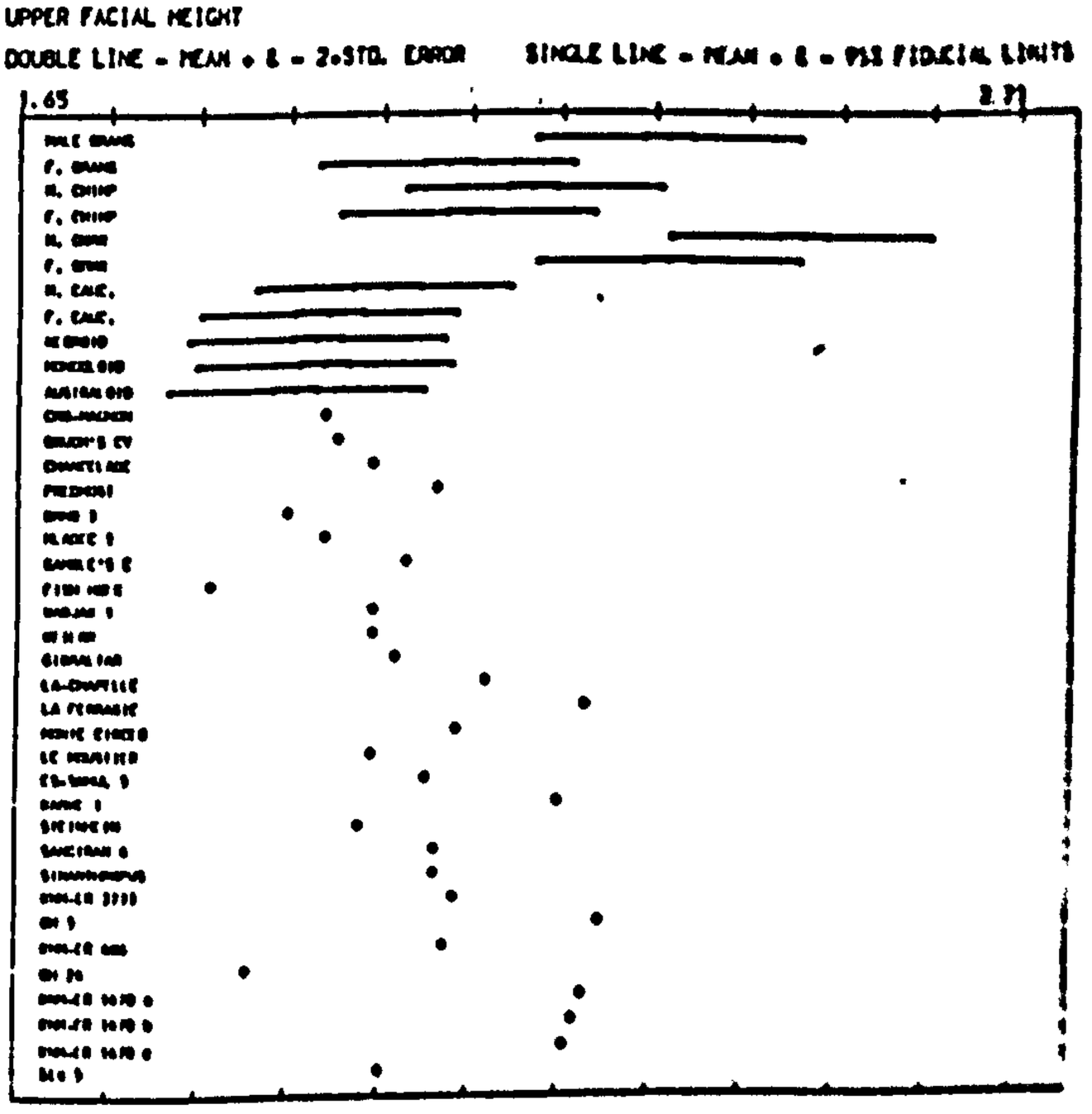
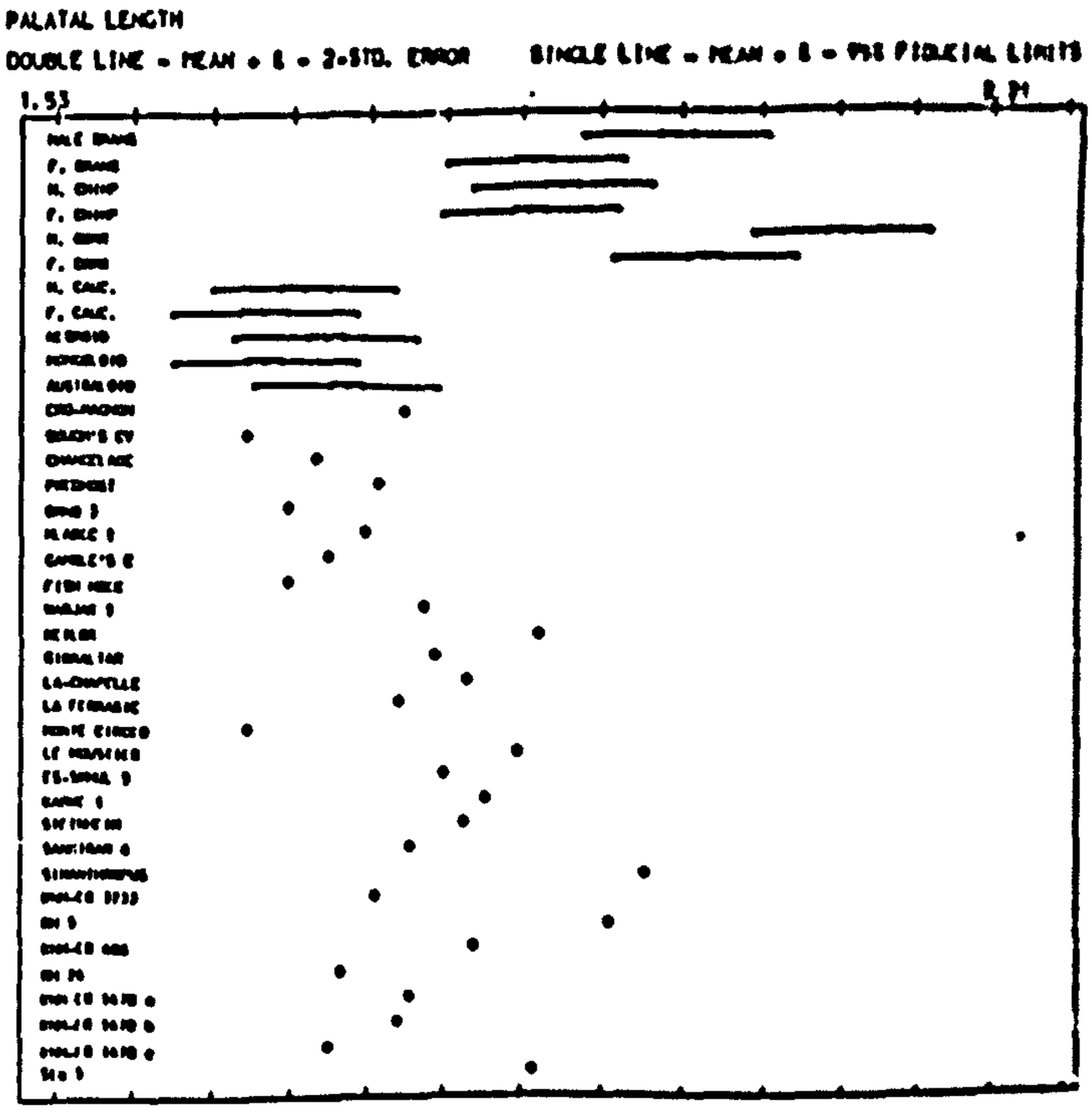




Figure C.8 – Univariate bar charts, pooled within group standard deviation, logged data.




PALATAL BREADTH
DOUBLE LINE = MEAN ± 2·STD. ERROR SINGLE LINE = MEAN ± 95% FIDUCIAL LIMITS

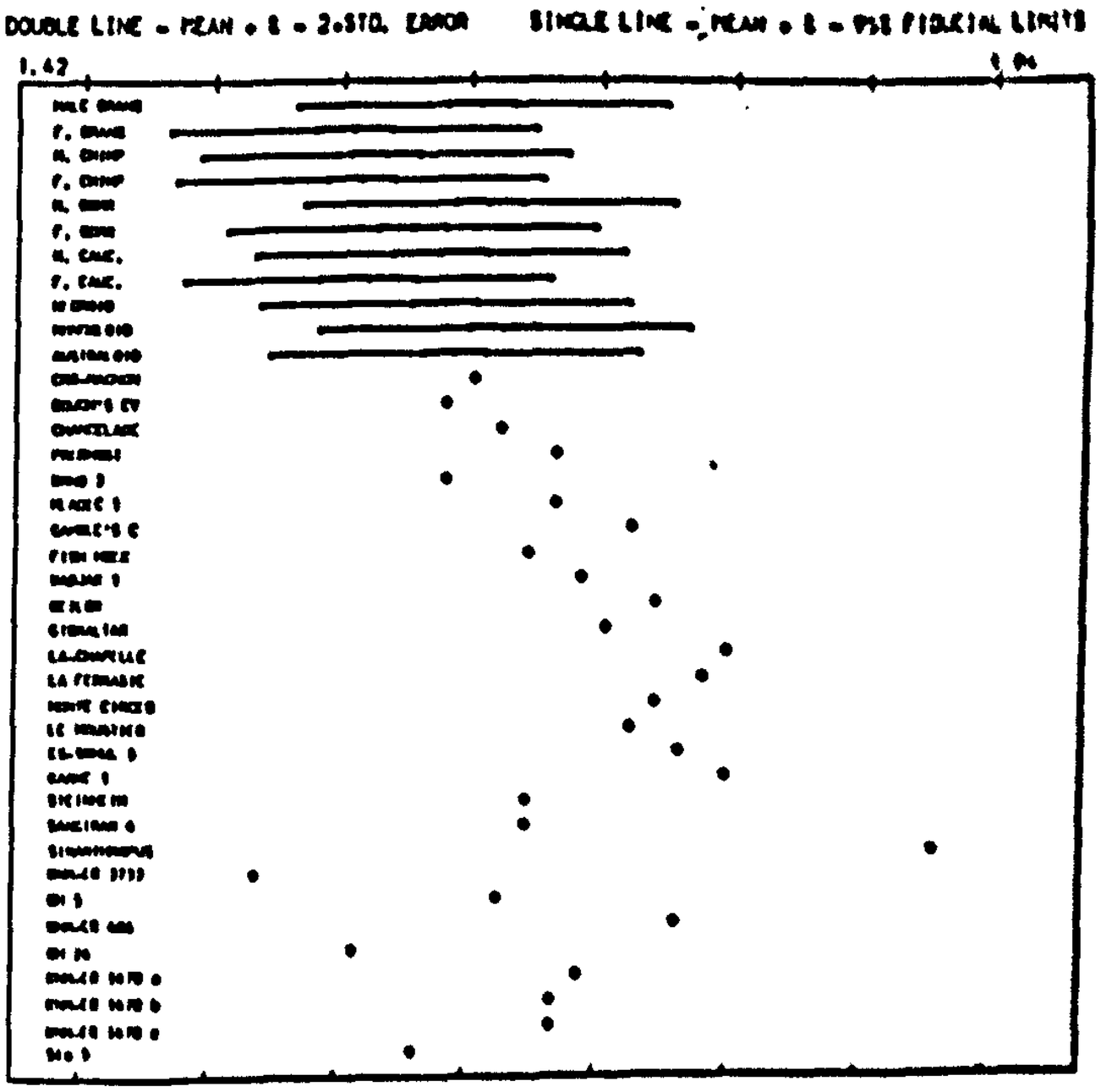
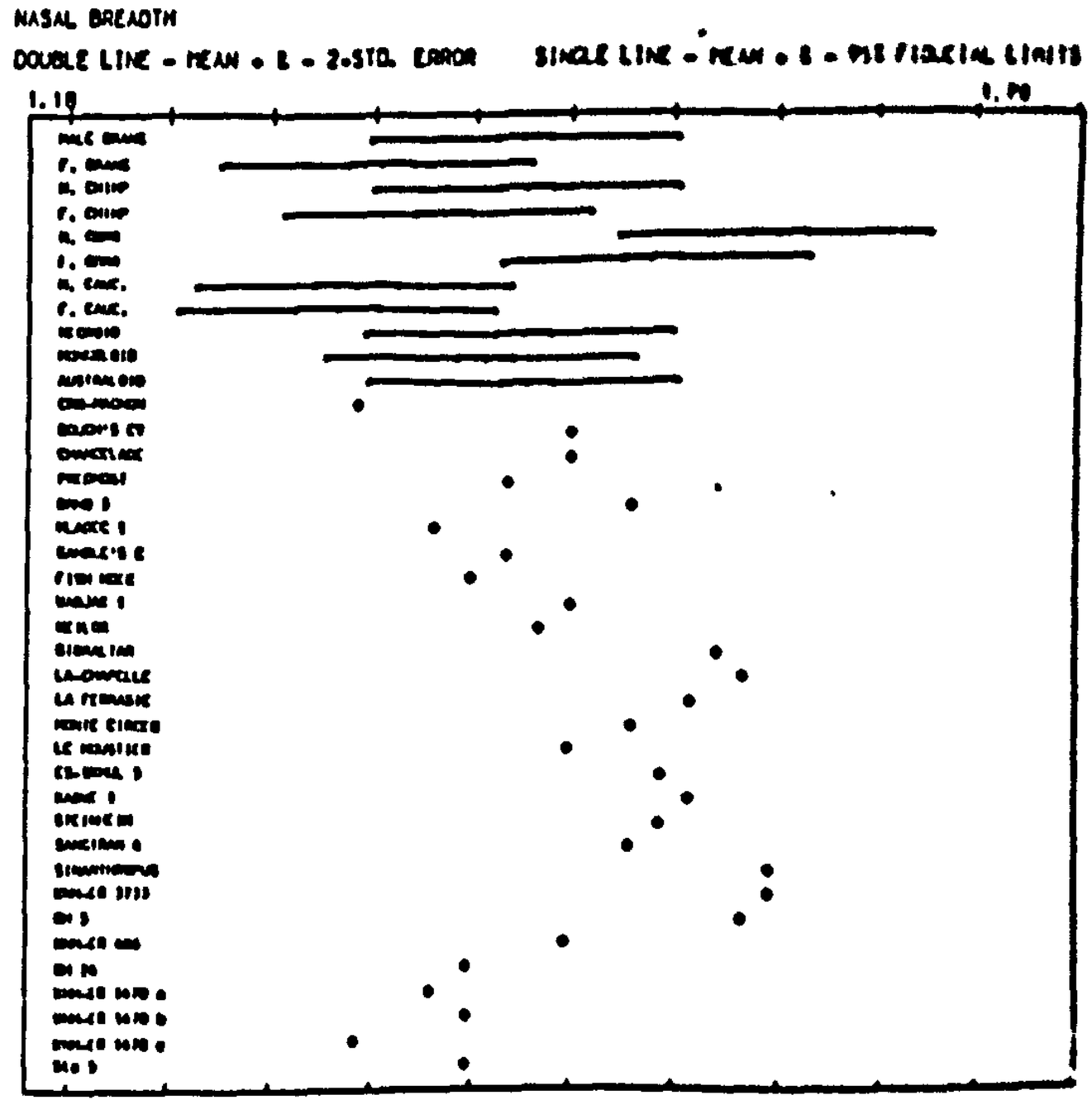



Figure C.9 – Univariate bar charts, pooled within group standard deviation, logged data.



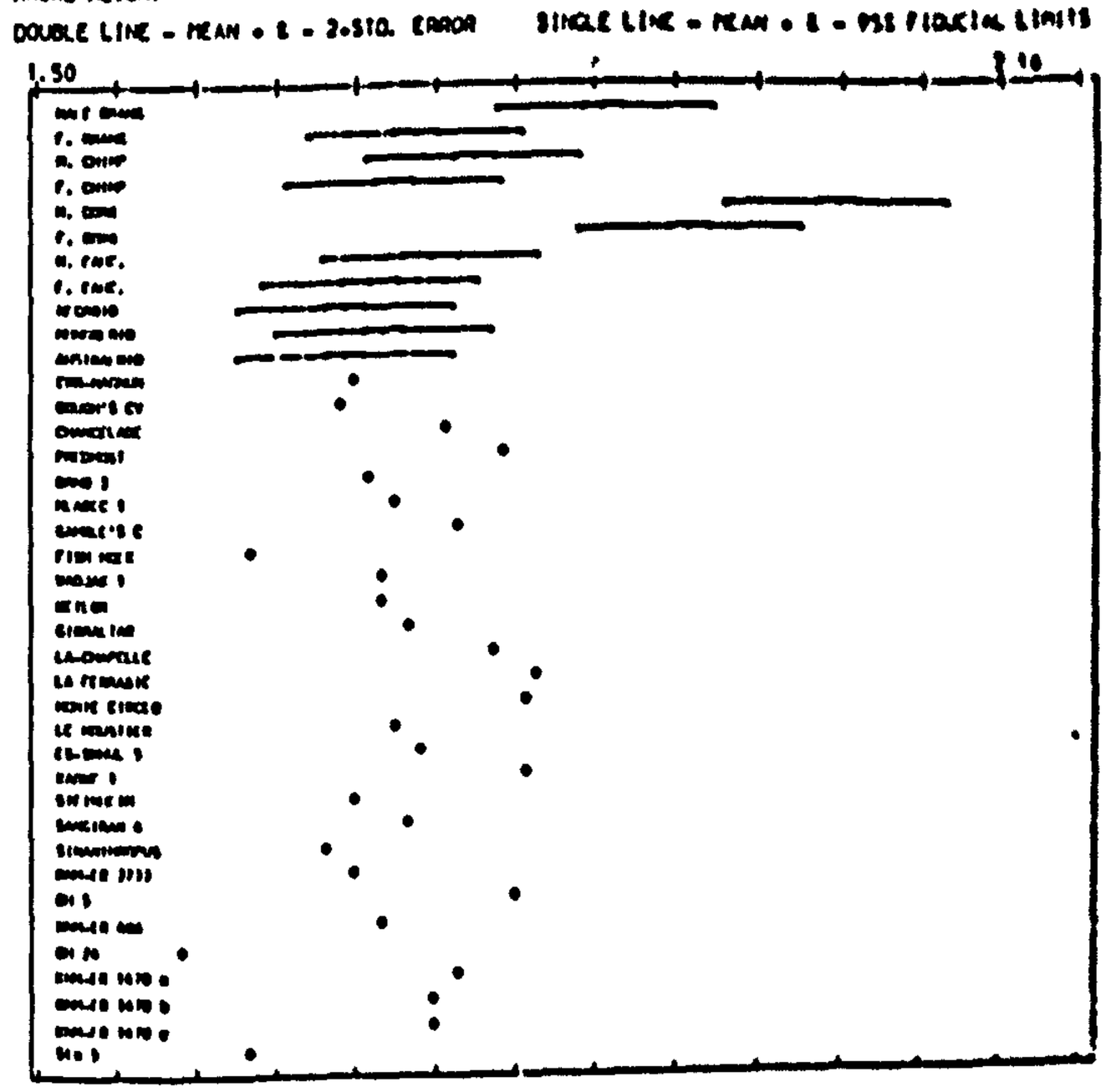
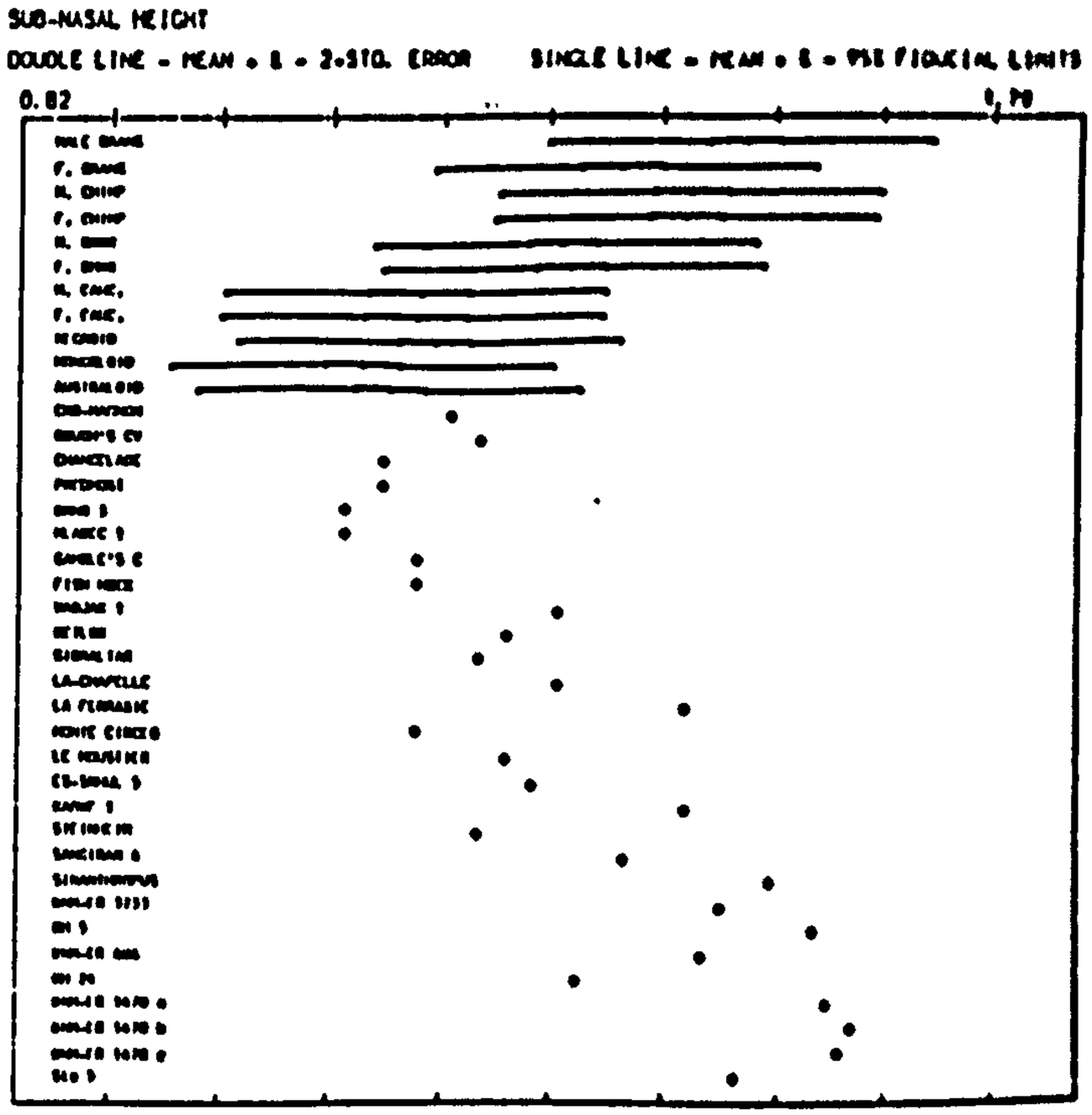




Figure C.10 – Univariate bar charts, pooled within group standard deviation, logged data.



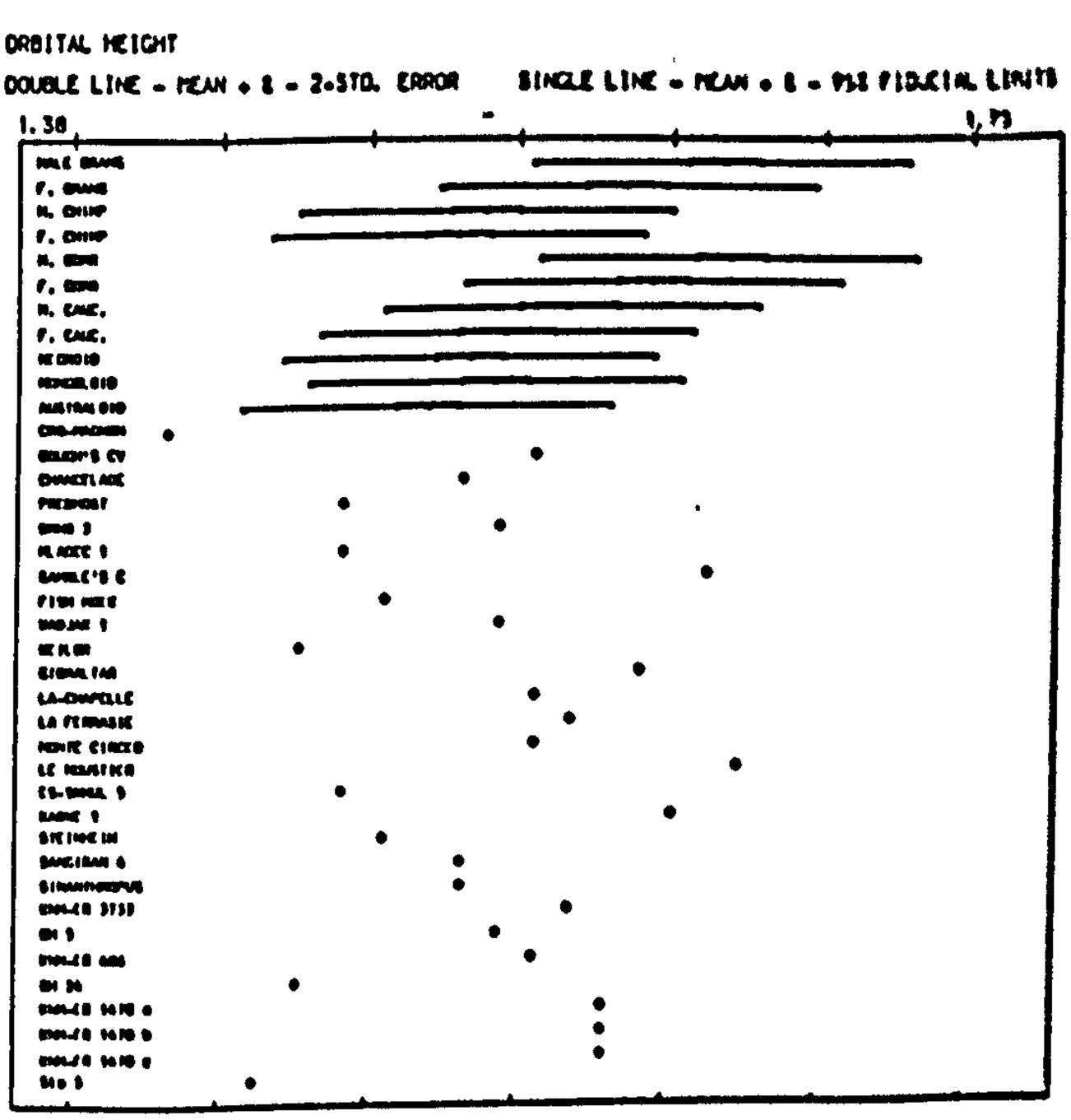




Figure C.11 – Univariate bar charts, pooled within group standard deviation, logged data.

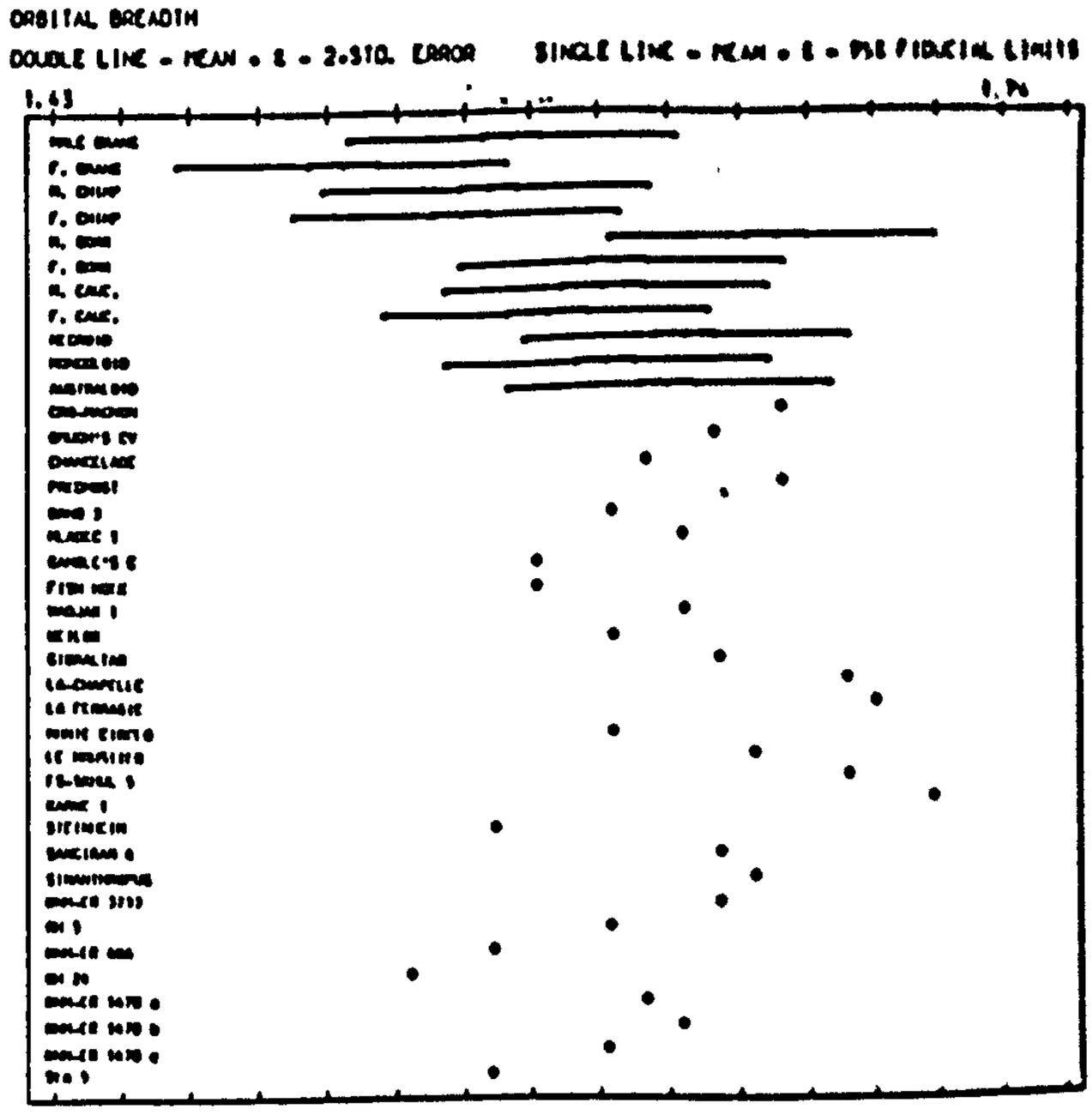
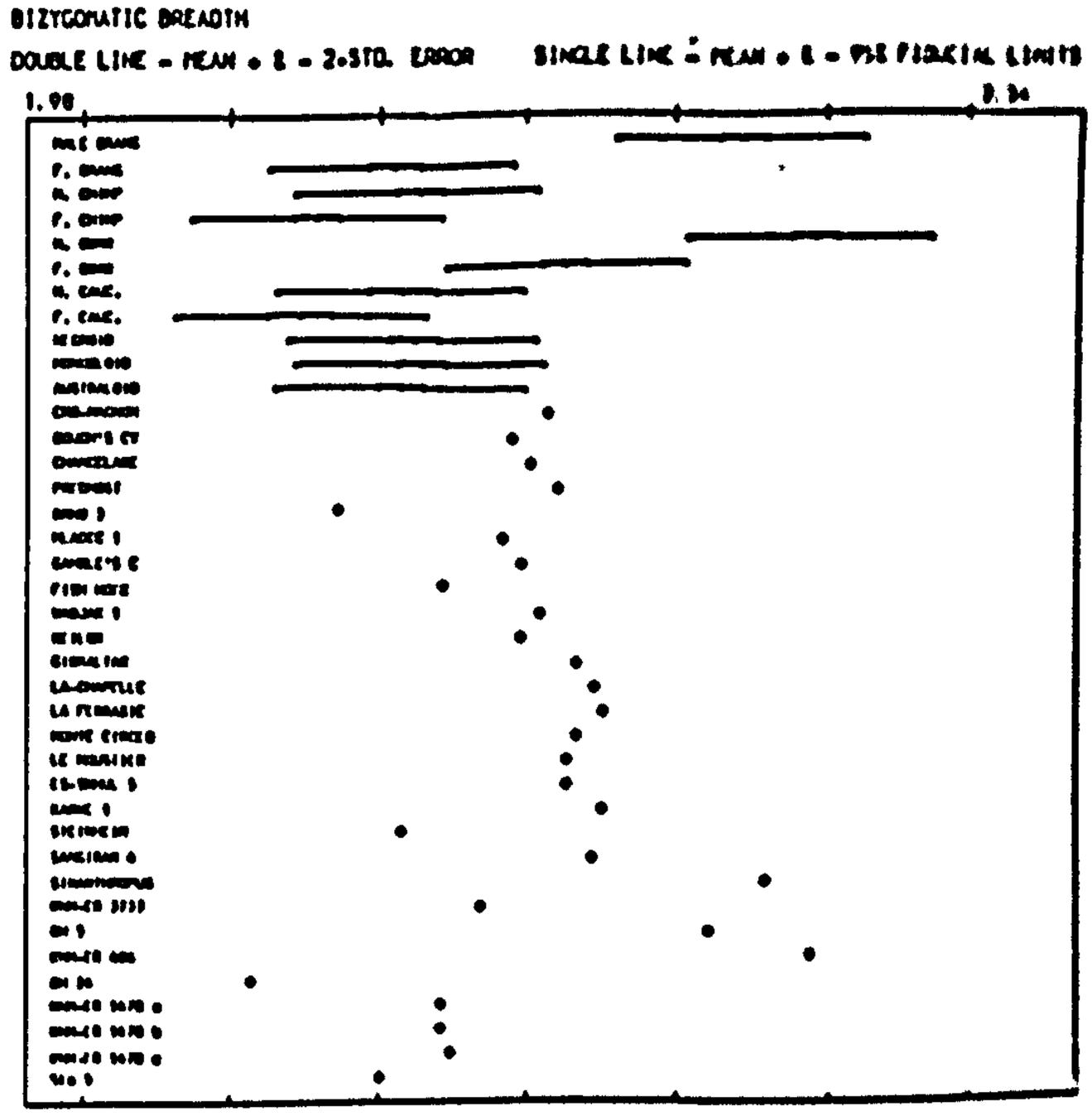



Figure C.12 – Univariate bar charts, pooled within group standard deviation, logged data.



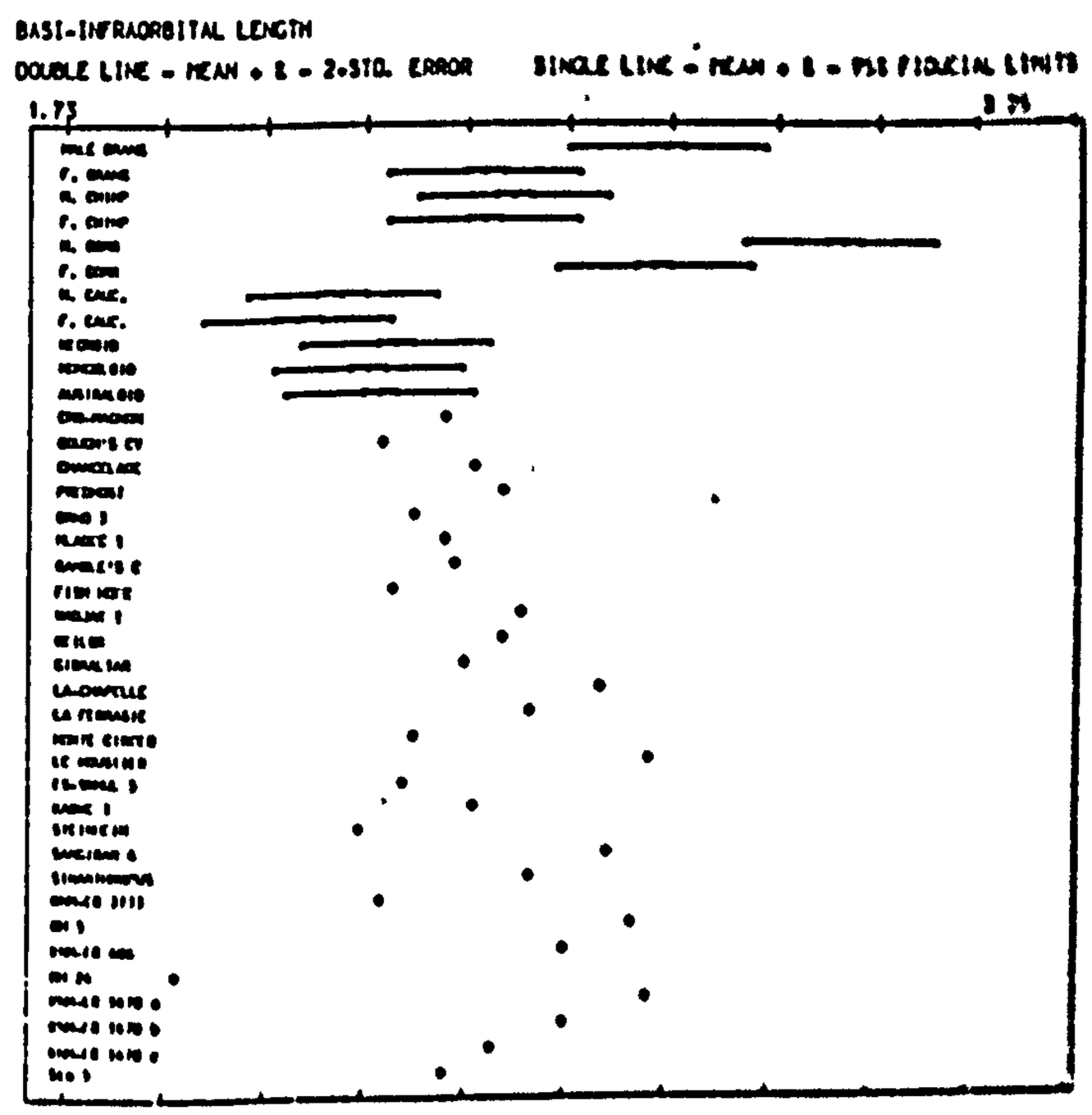
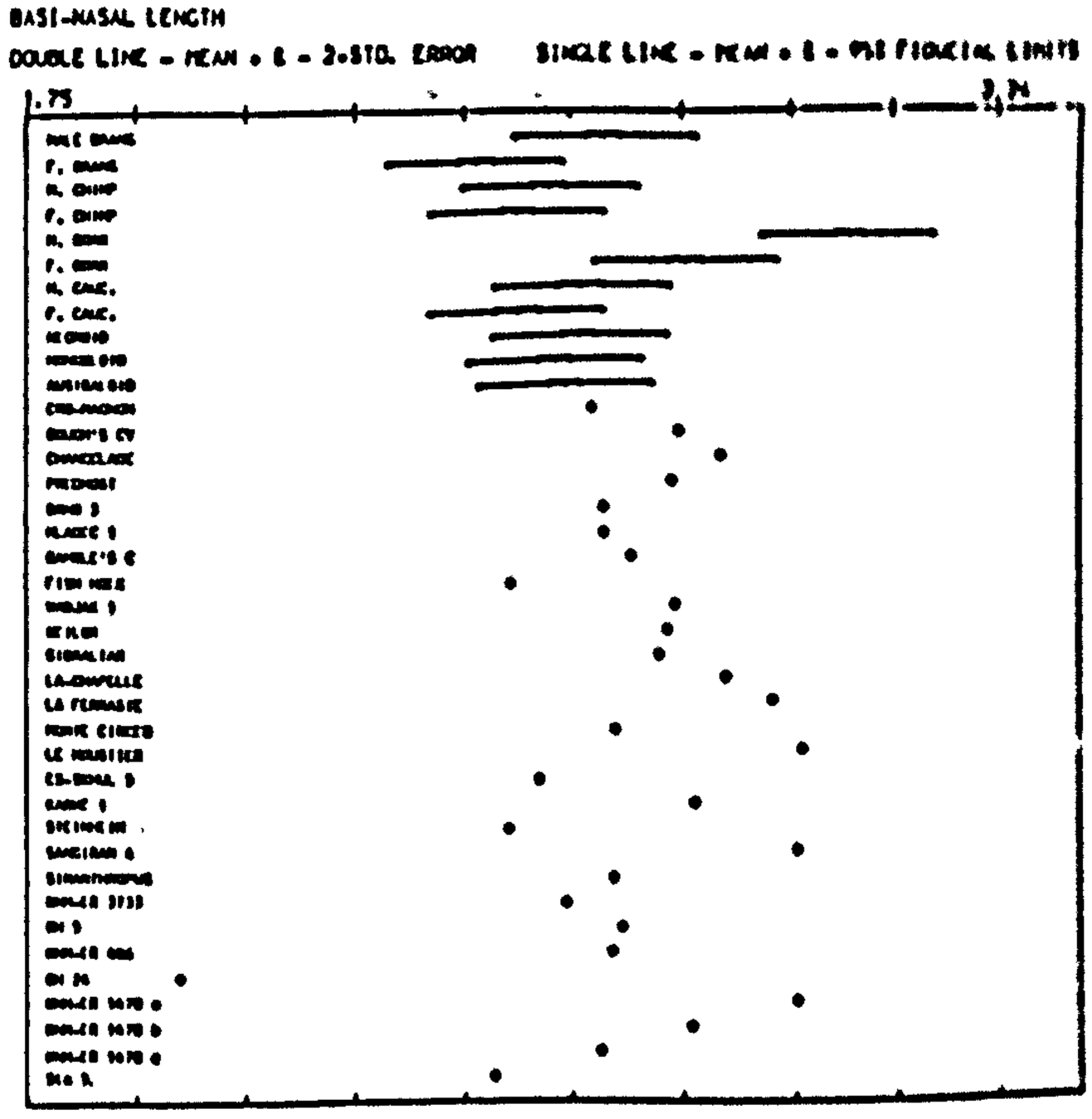




Figure C.13 – Univariate bar charts, pooled within group standard deviation, logged data.



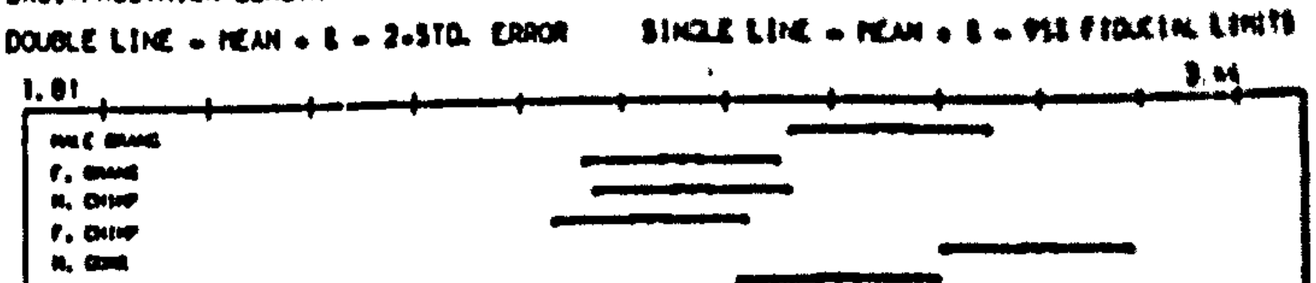
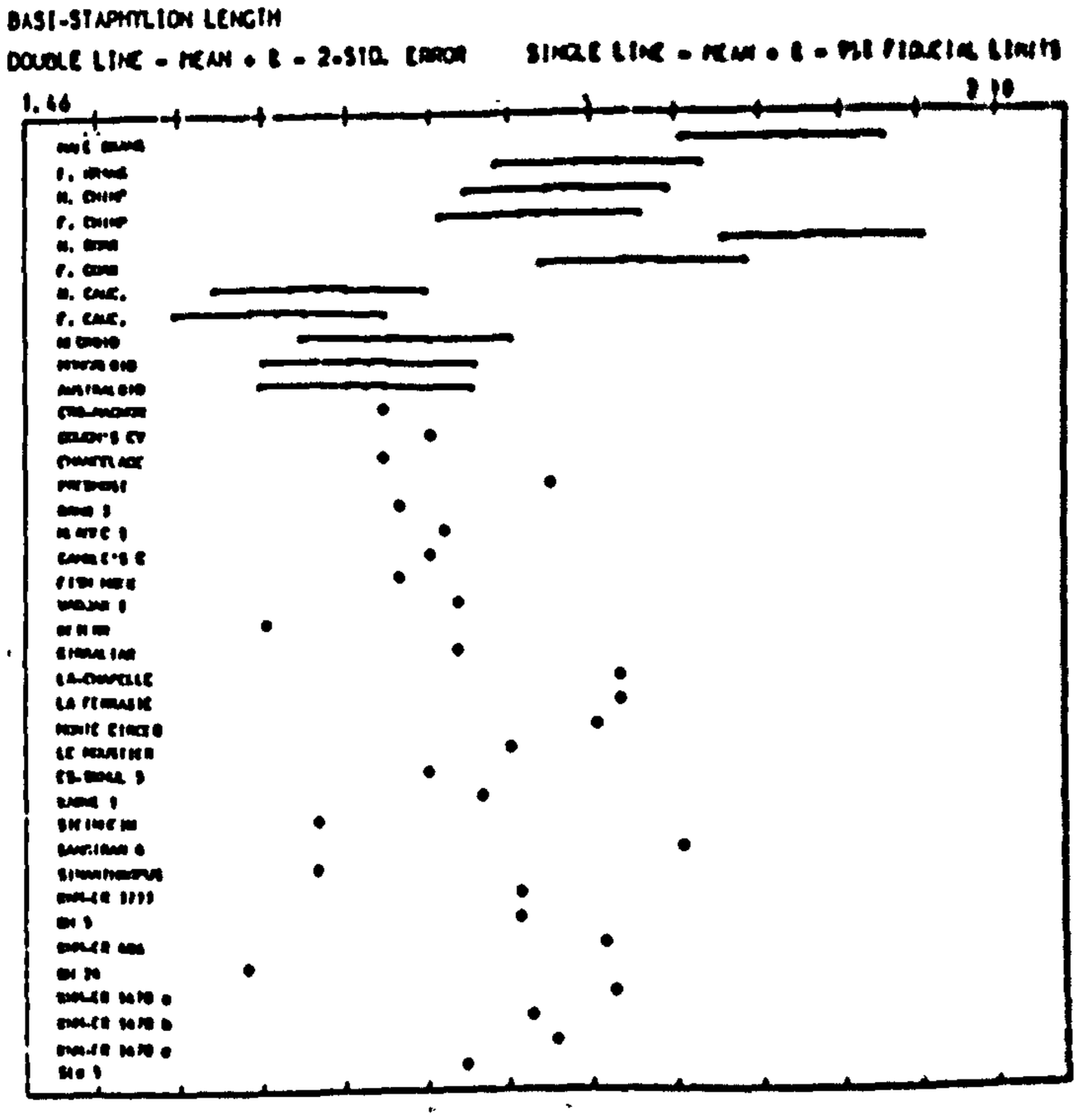




Figure C.14 – Univariate bar charts, pooled within group standard deviation, logged data.



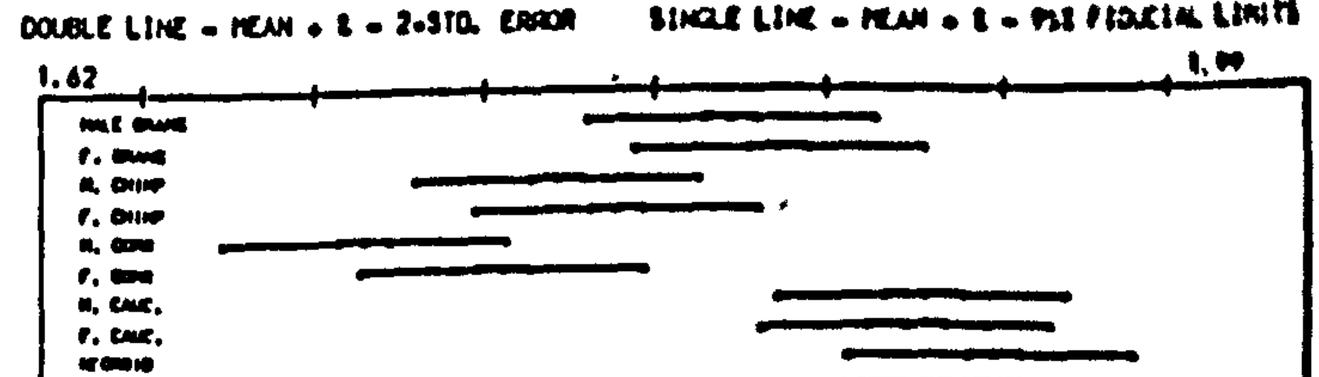




Figure C.15 – Univariate bar charts, pooled within group standard deviation, logged data.

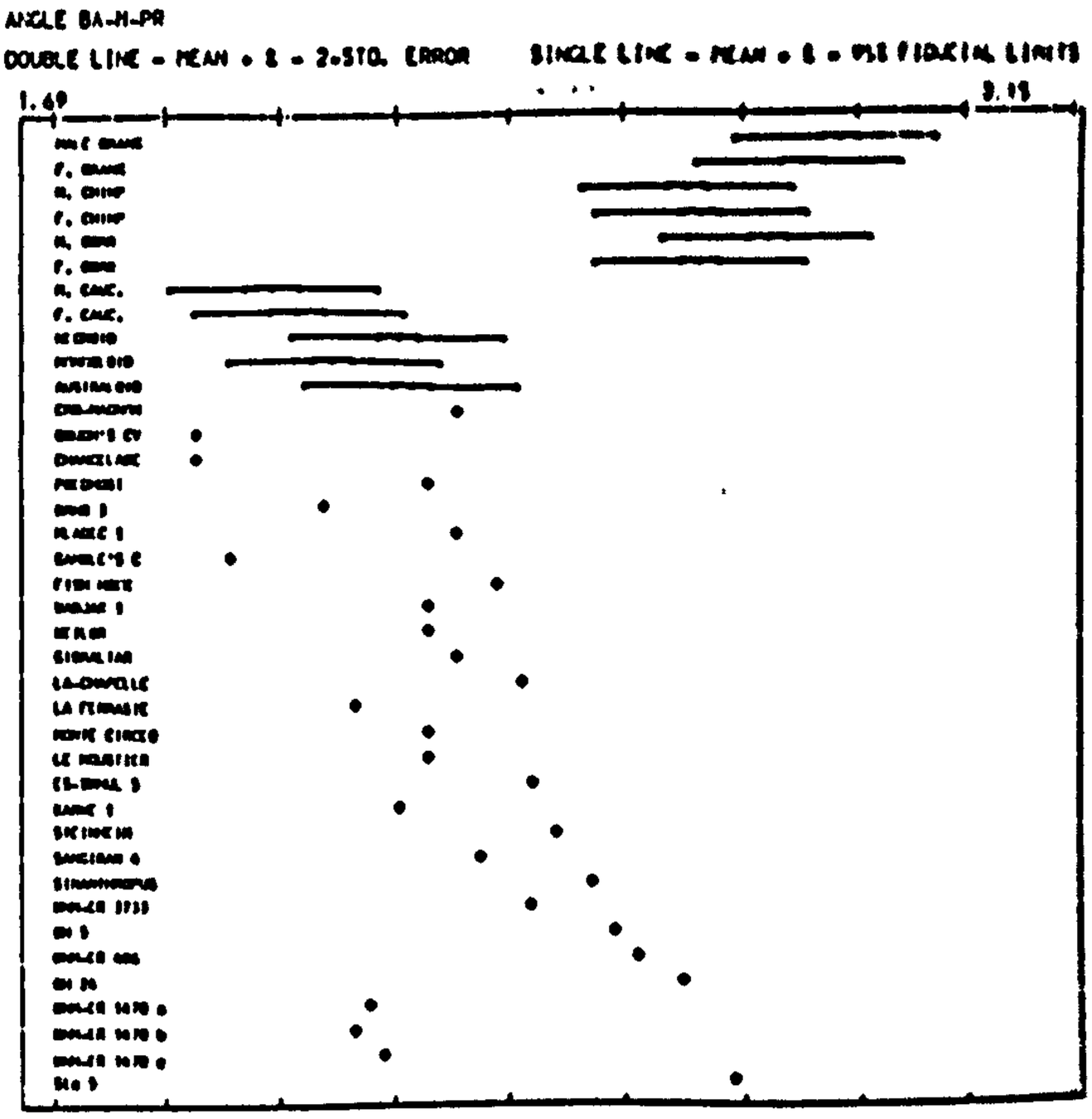



Figure C.16 – Univariate bar charts, pooled within group standard deviation, logged data.

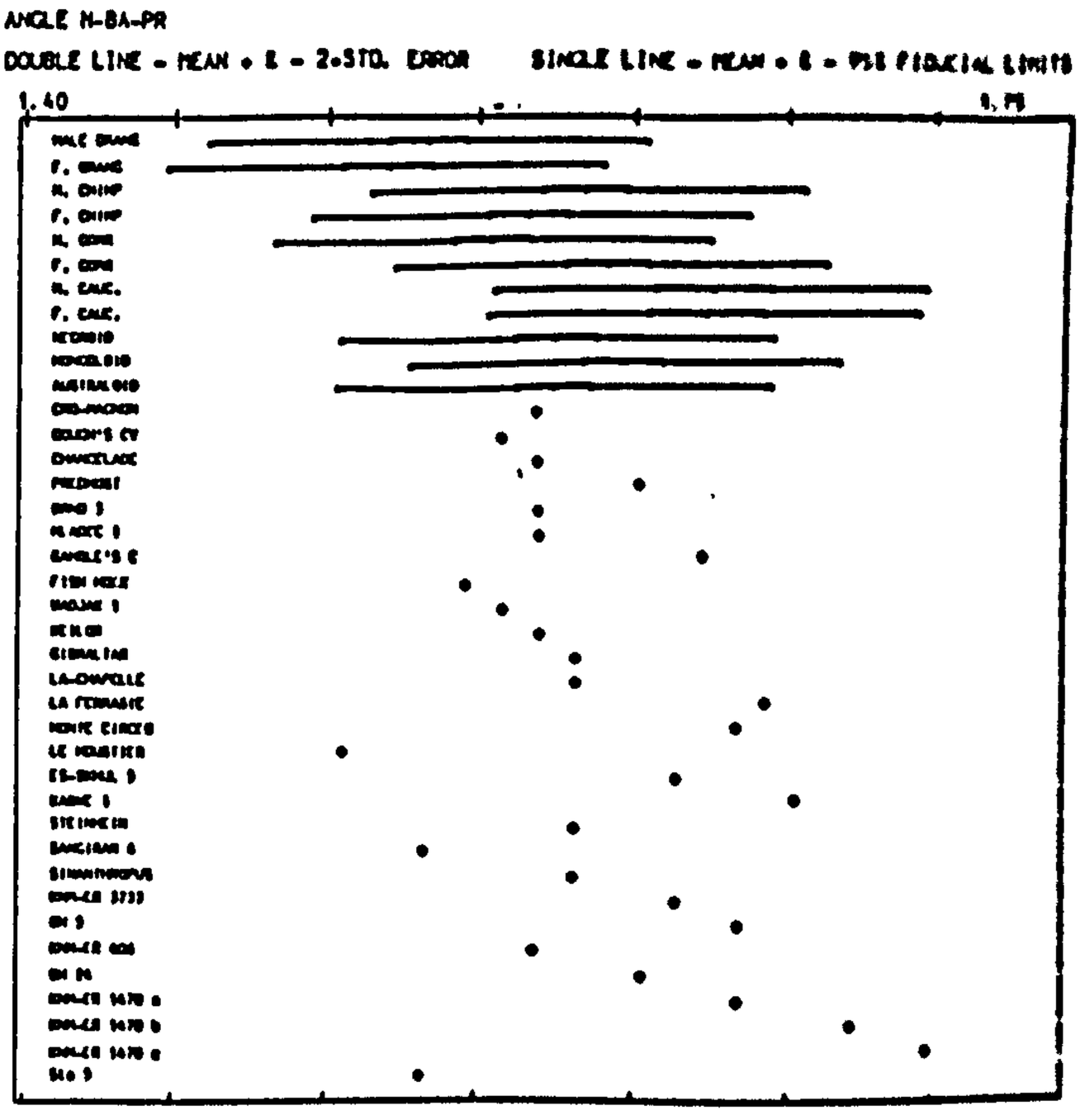



Figure C.17 – Univariate bar charts, pooled within group standard deviation, logged data.