THE METHODS OF QUANTITATIVE TAXONOMY WITH SPECIAL REFERENCE TO FUNCTIONAL ANALYSIS

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Abstract of

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ABSTRACT

The purpose of this thesis is to investigate the use of quantitative methods in taxonomy. Comparisons are made between several quantitative methods and the relative merits of these and the kinds of taxonomic information they produce are examined. To provide data on which to base these comparisons, measurements were made on the skulls of 20 hominoids and on the skeletons of 64 rodents.

The thesis consists of six chapters. Chapter 1 introduces the thesis. It discusses the nature of classification and outlines the changes which have taken place in taxonomists' views of the purposes for which classification is carried out. The recent view, that the purpose of classification is to provide a map of the diversity of organisms which is objective and has the maximum content of information is accepted and is used as a basis for evaluating the relative merits of the quantitative methods.

Chapter 2 considers the different stages involved in the use of quantitative methods and discusses the problems associated with each stage. The choice of forms and characters is briefly considered. The transformation

of characters is discussed and it is pointed out that although transformation is necessary when characters are measured in different units, transformation may also be used when characters are measured in the same unit to increase the sensitivity of coefficients of similarity to particular components of resemblance. The theoretical properties of five coefficients of similarity are considered. These are the correlation coefficient, the cosine of the angle between two forms, the mean character difference, the mean square distance and Penrose's shape coefficient. A geometrical model is used in the interpretation of these coefficients and it is pointed out that each is a legitimate measure of similarity. When comparisons are based on morphological characters, overall resemblance may be divided into size and shape components. It is shown that the five coefficients differ in their sensitivity to size components of resemblance and that the cosine of the angle, the correlation coefficient and Penrose's shape coefficient are less sensitive than the two distance coefficients to differences in size. Four methods of analysing tables of similarity values are examined. Three of these are methods of cluster analysis. These differ in the way in which they define similarity between

groups and in the relative weight they give to the members of groups. One of these methods is based on a new definition of the similarity between groups - the distance between their centroids. The fourth method examined is principal components analysis. It is pointed out that this method may be applied to both angular coefficients (e.g. the cosine of the angle and the correlation coefficient) and distance coefficients. The investigation of relationships by means of a principal components analysis of covariances between characters is discussed.

In Chapter 3, comparisons between the quantitative methods discussed in Chapter 2 are made using data obtained from 20 hominoid skulls. 99 characters of the skulls were expressed in quantitative terms. Three criteria were used in choosing these characters. Firstly, an attempt was made to choose characters from all parts of the skull; secondly, non-varying characters were ignored; thirdly, a functional approach to character definition was used. The problem of character transformation is discussed and it is shown that even a relatively simple transformation such as standardisation has a profound effect upon the coefficients of similarity. It is

suggested that, even when all characters are measured in the same unit, standardisation is useful since the patterns of relationship based on standardised character values are more informative than are those based on unstandardised values.

The five similarity coefficients are compared and the patterns of relationship produced by these are shown to be very similar. The most marked variations are found in the patterns produced by distance coefficients and these variations are attributed to the greater sensitivity to differences in size shown by these coefficients. Of the five coefficients, the correlation coefficient produces the pattern of relationships most similar to that arrived at by intuitive methods.

Three methods of cluster analysis are compared. These are the weighted and unweighted average pair-group methods, and a new method, the unweighted centroid pair-group method. The two methods which give equal weight (unweighted methods) to the members of clusters when measuring the similarity between clusters reproduce the tables of similarity values more faithfully than the method which gives greater weight to forms which join the clusters late in the clustering process. The method of principal components

analysis is applied to tables of correlations and mean square distances. The results of these analyses show good agreement with those produced by cluster analysis. Principal components analysis, however, provides more information about the inter-relationships of individual forms and gives a more accurate representation of the similarities between the forms than does cluster analysis.

Chapter 4 summarises the information provided by the quantitative methods about the phenetic relationships of the hominoid skulls. Twelve of the skulls represent the three genera of large apes and modern Homo sapiens. Each group is represented by a male, female and juvenile skull. Eight of the skulls are of fossil forms from the evolutionary line leading to modern H. sapiens. All methods point to a clear separation between the skulls of modern H. sapiens and those of the apes. The pattern of relationships within the ape group varies according to the coefficient used to measure similarity and only in the pattern based on the correlation coefficient do the males and females within each genus link together. The quantitative methods give a clear indication of the relative effects of differences in sex and age among the skulls of the four modern groups. The results of the

quantitative methods show a closer similarity between the chimpanzee and orang skulls than between these and the skull of the gorilla. The use of quantitative methods in analysing the relationships of the fossil skulls is considered and it is shown that the pattern of relationships among the fossil skulls is in good agreement with that based on intuitive assessments of resemblance.

Chapter 5 presents the results of a quantitative study of phenetic relationships among 25 species from 7 families of rodents. 244 characters of the skeletons of 64 individuals were expressed in quantitative terms. The similarities between skeletons were measured by means of the correlation coefficient and the square root of the mean square distance coefficient. The resulting tables of similarity values were analysed by means of the unweighted average pair-group method of cluster analysis. Covariances between characters were calculated and these were analysed by means of principal components analysis. It is shown that the correlation coefficient produces a more informative picture of the relationships between the forms than does the distance coefficient. Neither coefficient produces a pattern of relationships in complete agreement with the existing taxonomic arrangement of the forms. The relationships

shown by the correlation coefficient correspond to similarities and differences in functional adaptation whereas those shown by the distance coefficient correspond more to similarities and differences in overall size. The principal components analysis of covariances between characters provides more information about the inter-relationships of the forms than do the cluster analyses of similarities between the forms. The differences and similarities in diversity within and between the 7 families are clearly shown in the results of the principal components analysis.

The final chapter gives the main conclusions which can be drawn from the studies reported in the preceding chapters.

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1 INTRODUCTION

1.1 The nature and purposes of classification

Classification, the arrangement of things into groups or classes, is a fundamental human activity. For, as Simpson (1961, p.2) emphasises,"there could be no intelligible language if each thing (or each perception) were designated by a separate word, and no rational thought if symbols did not generalise characteristics and relationships shared by innumerable different objects". Such a need for systematisation of subject matter is particularly great in biology because of the vast numbers and bewildering diversity of animals and plants. There are, however, many possible arrangements of organisms depending upon the particular characters and relationships of organisms which are considered. The arrangement chosen by a taxonomist depends upon the purpose for which he is constructing the classification.

The opinions of taxonomists as to the purposes for which classifications are constructed have changed considerably since the earliest attempts at classifying organisms were made. The earliest classifications were based on Aristotelian logic and were attempts to portray the "natural affinities" of organisms. With the general acceptance of the theory of

evolution, however, the views of taxonomists changed and the primary purpose of classification was considered to be the depiction of evolutionary relationships. Recently, many taxonomists have put forward the view that the study of evolutionary relationships is a separate activity from that of classifying organisms and that the primary function of this is to organise our knowledge of organisms into a system which is stable, objective and of use to as many people and for as many purposes as possible. For example, Heslop Harrison (1962, p.14) says, "there can be few biologists who would not accept as one of the primary functions of biological systematics the production of a general classification of living things possessing at once the greatest possible content of information and the maximum convenience in use. Whatever other functions may be attributed to taxonomy - such, for example, as investigating phylogeny - this one, the creation of a data storage and retrieval agency is surely the inescapable one". This gradual change in the opinions of taxonomists has been accompanied by attempts to use more objective and explicit methods in constructing classifications. These attempts have culminated in what Cain (1959b, p. 241) has called the New Taxonomy, which is characterised by a "considerable revision of the whole basis of taxonomic theory, especially the relation of phylogenetic to natural classifications, a clear separation of

phylogenetic weighting from recognition of co-variation of characters, and the development of methods for making comparisons, whether phyletic or natural, more precise".

The basis of the modern view of taxonomy is more easily understood if the reasons for the modification of the earlier views are considered. Cain (1958) has stressed that the most important change in taxonomic theory that has occured has been the gradual abandoning of attempts to set up classifications on a priori principles agreeable to the rules of logic and some particular theory and the partial substitution of an empirical attitude. The use of a priori principles stemmed from Aristotle's method of logical division in which a set of objects was subdivided on the basis of their "essential natures". By the essence of a thing Aristotle understood the set of fundamental attributes which are the necessary and sufficient conditions for a thing to be of its particular type (Cohen and Nagel, 1934). However, although the Aristotelian scheme provides an elegant set of formal rules for the systematisation of a subject matter, it can only be applied successfully to objects whose essential natures are already known. But organisms cannot be defined in an Aristotelian sense since their essential characteristics are unknown and logical division is therefore impossible. It is only possible to proceed empirically, simply finding out what objects exist and

what are their attributes, and using these, without prior notions of their relative importance, in the formation of classes. The process of division from above, by means of a sequence of characters, must be replaced by a process of clumping organisms into groups, these into larger groups and so on. This point was clearly recognised by the botanist Adanson (1727 - 1806) who rejected the weighting of characters on *a priori* principles and put forward the view that classes should be based on the 'natural affinity' between organisms by which he meant their overall resemblance. This is measured by taking all characters into consideration (see Sneath, 1957 and Cain, 1959a and b). The prestige of *a priori* reasoning was so great, however, that Adanson's views were rejected. Nevertheless, in practice, although taxonomists were able to carry out division they could only do so using principles drawn from observation of groups previously constructed by an ascending method (i.e. the formation of classes on the basis of the resemblance of forms).

The opinions of taxonomists as to the purpose for which classifications are constructed changed following the general acceptance of the theory of evolution. Darwin put forward the view that "the Natural System of classification is founded on descent with modification; - that the characters which naturalists consider as showing true affinity between

any two or more species, are those which have been inherited from a common parent, all true classification being genealogical; - that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike" (Darwin, 1891, p.346).

This view, that the purpose of classification is to reveal the genealogical relationships of organisms, became widely accepted. When an extensive fossil record is available for a group of organisms it may be possible to indicate phylogenetic relationships by putting together those forms which most resemble each other. Even then, it is necessary to consider carefully the meaning of "resemble". When a fossil record is not available, as in large parts of the plant and animal kingdom, this method of exploring phylogenetic relationships cannot be used and inferences must instead be drawn from present-day material. However, morphological similarity cannot be regarded as an exact index of phylogenetic relationship: organisms evolve at different rates and organisms from different lineages may evolve in the same direction. Bigelow (1956, p.145) in a discussion of the bases of classification says "if all species had always been evolving at the same rate, then recency of common ancestry would

correspond with overall similarity. There is ample evidence, however, that rates of evolutionary change have varied and fluctuated both within and between evolving phyletic lineages. In the course of time, these different fluctuating rates of change must have produced complex overall differences which do not correspond with recency of common ancestry. Clearly overall similarity and recency of common ancestry are two separate and distinct phenomena which must be considered separately".

If the concepts of "essential nature" and "phylogenetic relationship" cannot be accepted as general bases for classification, what should the purpose of classification be? Gilmour and Walters (1964, p.11) summarise the view held by many taxonomists as follows: "we suggest that this purpose be consciously and openly accepted as the making of a broad map of the diversity of living things which, by taking account of as wide a range of attributes as practicable, will serve the needs of as many as possible of those concerned with plants and animals". Gilmour considers classifications which serve a wide range of purposes to be "natural" classifications. Although this use of the term natural has been questioned by some taxonomists (see, for example, Simpson, 1961) it corresponds to the sense of naturalness held intuitively since before Darwin. The reason for the great usefulness of

natural classifications is that the members of their classes possess many attributes in common and therefore the "implied information" is high (Sneath, 1957) and many generalisations may be made about these members.

Since natural classifications are systems of classes whose members show a high degree of overall resemblance, their construction depends to a large extent on the judgment of similarity between organisms and groups of organisms. Up to the present, however, this judgment has usually been subjective and there are only a few examples of attempts to analyse and express affinity in more objective terms. The current critical discussion of the aims and practices of taxonomy (see, for example, Sokal and Sneath, 1963) has led to a renewal of interest in these objective methods of judging similarity and constructing classes and has led to the development of new ones. These methods, which attempt to make the judgment more explicit and, in addition try to express degrees of similarity in numerical terms, are beginning to have a wider application in taxonomy. They are of particular importance in fields of taxonomy where judgments are controversial.

1.2 The purpose and scope of the thesis

The taxonomist who wishes to use quantitative methods in

the study of relationships and for the construction of classifications is faced with a number of problems. For example, what characters should be employed in describing the organisms to be classified and how should these characters be coded and transformed; what are the relative merits of the different coefficients used to measure similarity and what kinds of taxonomic information do these produce; what are the best methods of recognising and defining taxonomic groups from tables of taxonomic affinities; what conclusions can be drawn from numerical studies about, for example, functional and evolutionary relationships?

The purpose of this thesis is to discuss some of these problems and to compare several of the more recently developed methods in action. To provide data on which to base these comparisons, measurements were made on 20 hominoid skulls and 64 rodent skeletons.

The purpose of Chapter 2 of the thesis is to consider in more detail some of the quantitative methods which have been suggested for use in classification. This discussion is followed in Chapter 3 by a comparison of the various methods in action, with an examination of the differences in outcome and a consideration of possible reasons for these differences. In Chapter 4, the phenetic relationships of the hominoid skulls revealed by the quantitative methods are discussed and the

use of quantitative methods in the investigation of hominoid evolution is briefly considered. In Chapter 5, quantitative methods are compared in a study of phenetic relationships among rodents. In the final chapter, the main conclusions of the thesis are given.

The arrangement of figures and tables is as follows: each figure is placed in the text immediately following the page on which it is first cited; the tables, however, are placed at the ends of the chapters in which they are first cited.

2 QUANTITATIVE METHODS IN TAXONOMY

2.1 Introduction

The arrangement of forms (organisms or groups of organisms) into a classification can be divided into a number of stages. The first is the choice of forms and the choice of characters on which to base the comparisons between the forms. When the characters are measured in different units, a transformation of the character values is necessary. In addition, the taxonomist may find it useful to transform the character values in order to study the effects of a factor such as size. The third stage is the measurement of the similarity (= overall resemblance) between pairs of forms and this is followed by an analysis of the similarities between all pairs of forms in order to reveal the groupings present.

These stages produce a <u>phenetic</u> classification. Whenever possible, the biologist wishes to follow this arrangement of forms in a phenetic classification by asking whether any conclusions can be drawn about the evolutionary relationships of the groups. That is, he wishes to follow the study of phenetic relationships by one of phyletic relationships. A final stage, the examination of character values within and between the groups produced may help in studying the evolutionary relationships

between the groups. The purpose of this chapter is to consider each of these stages in detail, to point out some of the problems associated with them and to provide a framework on which to base the comparisons between the methods which form the subject of Chapter 3.

2.2 The choice of forms and characters

In a discussion of the taxonomist's judgment of affinity, Cain and Harrison (1958) emphasise that the units which form the subject of a classification can be of many different kinds. They may, for example, be different species recognised as such on biological grounds, samples of fossils from different localities or strata, different populations defined geographically and so on. In fact, as Cain and Harrison point out, different forms are simply those entities which a taxonomist finds it useful to compare.

It is important, however, to distinguish between the situation in which no previous judgments are made about the units which are to be compared and that in which the units are considered to be representative of groups already recognised by other criteria. In the first case, as Williams and Lance (1965) point out, the units to be classified are members of a finite population: they are as completely defined as the taxonomist wishes, they are postulated as different, and any null hypothesis

that they are samples from a larger population is highly artificial. In the second case, it is essential for the taxonomist to decide whether the individuals are to be regarded as samples from a population and thus subject to error, or as convenient sources of information which define the groups sufficiently as distinct from merely illustrating them. Much of the discussion concerning the statistical significance of quantitative studies in taxonomy is confused by the failure to make the above distinctions. The points mentioned here will be illustrated in Chapter 3 when the choice of forms on which to base the comparisons between the methods is considered.

One outcome of recent discussions of the principles of classification has been the clarification of the concept of a taxonomic character. For example, Cain and Harrison (1958) define a character as "anything that can be considered as a variable independent of any other thing considered at the same time" (see also Cain, 1954). This wide definition is intended to include characters drawn from studies of, for example, morphology, physiology and behaviour; and many taxonomists now emphasise that comparisons should, if possible, be based on a wide variety of characters. The kinds of characters that can be used will depend upon the material available and when, as in the studies of hominoids discussed later, the analysis of relationships includes fossil forms, the choice of characters

is usually limited to those of the skeleton.

When characters are drawn from studies of, for example, physiology and behaviour, the way in which characters are defined is usually determined by the experimental techniques available to the taxonomist. In the case of comparisons based largely on morphology, however, the taxonomist is frequently presented with alternative ways of defining characters. For example, a taxonomist who wishes to describe the complex geometry of the mammalian skull may either abstract characters in an arbitrary manner or he may attempt to characterise the skull with some particular viewpoint in mind; for example, he may try to recognise functional units and frame his description of the skull accordingly. This approach to character definition can be justified on the principle that the resulting classification has a greater information content. A method of describing a skull which obscures features which may be biologically interesting is not incorrect but simply wasteful. For example, in the comparison between the skull of the male gorilla and that of man, one possible character is the maximum height of the skull perpendicular to the Frankfurt horizontal plane. A functional approach to the skull recognises that in the male gorilla a sagittal crest has formed because the surface of the brain case does not provide sufficient area for the insertion of the

temporal muscles. A functional approach would use several characters to describe "skull height" - for example, height of brain case, height of sagittal crest and maximum height of temporal musculature.

As Harrison and Weiner (1964, p. 78) point out: adaptation to an environment is achieved by changes in the way an organism functions and therefore the phenotypic units on which natural selection directly acts are obviously units of function. It seems reasonable therefore that one will get more phyletic information from such units than from morphological differences which have been abstracted arbitrarily. In mammals, at least, the functional significance of most structures is appreciated to some extent, and workers do on the whole make their comparisons with reference to function.

Besides considering the kinds of characters to include in a comparison, the taxonomist has to decide how many to use. Comparisons between groups of organisms have frequently been based on a single character or on a very small number of characters. These comparisons may be legitimate for some purposes but they are misleading if they are interpreted as measures of <u>overall</u> similarity. For, although all characters are presumably correlated to some extent, the information provided by one set of characters is not necessarily the same as that provided by another set. Although taxonomists agree

that overall comparisons should utilise many characters, the question of how many is not easily answered on theoretical grounds. Sokal and Sneath (1963, p. 115) admit that there is as yet no unequivocal answer to this question. Rao (1954) discusses this problem with respect to one particular method of measuring overall resemblance, Mahalanobis's Generalised Distance Coefficient (D^2). He postulates the existence of a finite number of factors (which may be called genetic) which influence all characters and sets up a simple model in which if $v_1, \ldots, v_k$ denote the effects of these factors for any individual, the value x_i of the i-th character is determined by:

$$x_i = a_{1i} v_1 + \ldots + a_{ki} v_k + e_i$$

where e_i is a random component (which may be thought of as the effect of environmental factors) which is independent of $v_1, \ldots, v_k$ and where the coefficients $a_{1i}, \ldots, a_{ki}$ specific for the i-th character are the same for all groups under consideration. Rao shows that, for this model, the value of D^2 tends to a finite value as the number of characters increases indefinitely. However, further research is needed in order to show that the assumptions on which the use of Generalised Distance and the construction of Rao's model are based hold for taxonomic comparisons in general. This point is considered further in Section 2.6.

One criterion which can guide the taxonomist in his

choice of characters and help him to determine the number of characters on which to base his comparisons is discussed by Cain and Harrison (1958). They point out that "it is customary to say of two forms that they are identical as far as is known except in the characters w, x, y, etc. It is then unnecessary to measure thousands of characters in which these two are indeed for the purposes of the investigation identical". Identity between two forms is more easily defined as lack of any difference between them than by enumerating all possible characters and recognising that each of these is the same in both forms. A measure of the degree of overall difference between two forms is thus obtained rather than a direct measure of their degree of overall similarity.

2.3 Transformation of character values

Cain and Harrison (1960) define a phenetic classification as "an arrangement by overall similarity, based on all available characters without any weighting" and contrast it with a phyletic classification which aims to show the course of evolution. Character weighting is necessary in order to produce a phyletic classification and the distinction between the two types of classification has usually been based on the presence or absence of weighting. However, even when the aim is only to study phenetic relationships, all available characters are not

used and transformation of the characters on which the comparisons are based may be necessary. The selection and transformation of characters may involve judgments about the relative importance of characters and are then forms of character weighting. However, they differ from the weighting procedures used in constructing phyletic classifications because they use objective and explicit methods for determining character weights.

The selection of characters was considered in Section 2.2. Characters which do not vary over the forms studied are of no importance for the purpose of estimating overall difference (which is considered to be the simplest method of measuring affinity) and should therefore be given zero weights. If non-varying characters are not excluded, the powers of discrimination of those coefficients which express affinity as mean difference per character will be decreased and quite large differences between forms will be obscured in the estimates of affinity.

The characters chosen for a phenetic comparison are frequently measured in different units. For example, although most of the characters of the hominoid skulls used in this study were linear dimensions measured in millimetres, some were angles measured in degrees and others were qualitative aspects of the skull such as the development of parts of the nasal chamber; and these latter characters were divided into states numbered according to the degree of development of the parts.

The contributions of different characters to a measurement of overall resemblance should not depend upon the units in which the characters are measured and a transformation which provides each character with a common scale is necessary. One particular method suggested for use in quantitative taxonomy (see, for example, Sokal and Sneath, 1963, and Rohlf and Sokal, 1965) is standardisation in which the values of a particular character (for all the forms considered) are transformed so that their mean becomes the origin and their standard deviation the unit of measurement. The transformation is:

$$x'_{ij} = (x_{ij} - \bar{x}_i)/s_i$$

where x_{ij} is the raw value and x'_{ij} the transformed value of character i for form j; $\bar{x}_i$ and s_i are the mean and standard deviation of character i calculated over all the forms considered (see Table 2.1). It should be noted that standardisation may be thought of in geometric terms as the combination of a translation and a change of scale. Standardisation moves the origin of the character space (see Section 2.4) to the centroid of the cluster of forms and equalises the scatter of values of each character (about the mean of values for each character) by expanding or contracting each character axis.

A transformation may also be useful when characters are already measured in the same units. Ornstein (1965) in a discussion of the use of transformations in classifications

distinguishes between two kinds of transformation: reweighting and normalisation. The general purpose of reweighting is to reduce the magnitude of a special kind of similarity (e.g. redundancy) in the collection of forms to be classified. The attachment of zero weights (see p. 17) to non-varying characters is one example of reweighting. The translation of the origin of the character space to the centroid of the cluster of forms and the expansion or contraction of the character axes are two more examples. The consequences of these forms of reweighting are considered in the comparisons between the methods in Chapter 3.

The general purpose of normalising is to increase the sensitivity of a similarity measure to otherwise "hidden similarities" between forms. For example, when comparisons are based mainly on morphological characters, overall resemblance has two components: resemblance in size and resemblance in shape. The taxonomist may wish to remove the size component in order to study resemblances in shape. Several coefficients of similarity have been proposed which involve one or more normalising steps. These are discussed in Section 2.4.

2.4 Measurement of similarity

Techniques for measuring similarity may be divided into categories according to the kinds of characters with which they are best able to deal. Coefficients of association are designed to measure similarity when the characters take on only two states. When characters take on more than two states, as do all the characters used in this study, other coefficients are more suitable. A geometrical model helps in the interpretation of these coefficients of similarity. The forms studied may be thought of as points lying in a multi-dimensional space the axes of which correspond to the characters on which the comparisons are based. The relative positions of the points in this "character space" are determined by the particular character values each form possesses. For example, in Fig. 2.1, the position of form 1 with respect to characters i and j is determined by its value for character i (X_{i1}) and that for character j (X_{j1}).

The coefficients which may be used to measure resemblance when the characters take on more than two states may be divided into two groups. The first group consists of those coefficients which measure the angles between the lines connecting the points to the origin of the space. The second group consists of those coefficients which measure the distances (suitably defined) between the points (see Fig. 2.1).

Figure 2.1

Diagram to illustrate the geometrical interpretation of similarity between two forms. The upper line joining the two forms is the "city block" distance between them and this distance, when divided by the number of characters, is equal to the mean character difference. The lower line joining the forms is the Euclidean distance between them and, when divided by the number of characters, is equal to the square root of the mean square distance.


character i
form 1
x_{i1}
x_{i2}
form 2
x_{j1}
x_{j2}
character j

2.4.1 Angular coefficients

The use of the angle (between the lines joining the forms to the origin of the character space) as a measure of resemblance was first suggested by Bhattacharyya (1946) but it has only rarely been used in recent taxonomic studies. Edwards and Cavalli-Sforza (1964), in a study of relationships among a number of human populations, measured the resemblance between the populations by the angle between the points (representing the populations) on the surface of a unit hypersphere. All three workers measured the angle by its cosine and then transformed it: Bhattacharyya transformed it to the angle itself and Edwards and Cavalli-Sforza transformed it to a distance: $d = \sqrt{(2 - 2 \cos \theta)}$. In this study, the use of the cosine of the angle without transformation as a measure of resemblance is considered (for formula used in calculating this, see Table 2.1).

It was suggested in the previous section that when the characters used in making a comparison are mainly morphological, the taxonomist may wish to ask how much of the overall resemblance between two forms is a result of a similarity in size and how much is a result of a similarity in shape. One measure of size is suggested by the geometric model mentioned above. The distance of a point from the origin of the space may be thought of as a measure of the size of the form

represented by that point. Two points at different distances along a line through the origin represent two forms which differ only in size and, conversely, two points which are not on the same line but at equal distances from the origin represent two forms which differ only in shape. The angle (and therefore the cosine of the angle) between the lines joining two points to the origin is therefore a measure of the difference in shape between forms represented by these points. The points representing two forms will lie on the same line only if the character values of one are equal to the character values of the other multiplied by a constant factor. If X_{i1} and X_{i2} represent the value of the i-th character for forms 1 and 2 then these forms will differ in size only, if (for all i)

$$X_{i1} = kX_{i2}.$$

The cosine is therefore a measure of similarity which normalises for differences in <u>proportion</u> due to a constant multiplicative factor.

The term "size difference" is also used to describe the situation in which the character values of one form are equal to those of another <u>plus</u> a constant term. That is, two forms are said to differ in size only, if (for all i)

$$X_{i1} = X_{i2} + b.$$

A measure of similarity which normalises for multiplicative <u>and</u> additive factors is the <u>product-moment</u> correlation

coefficient. It is equal to the cosine of the angle between two forms when the character values of the first form are expressed as deviates from the mean of all the character values of that form and the character values of the second are expressed as deviates from the mean of its character values. The formula used in calculating the correlation coefficient is given in Table 2.1.

The correlation coefficient has been suggested as a measure of resemblance simply on the grounds that it is a measure of covariation: if the changes in values from character to character in one form are paralleled by those in a second, the correlation coefficient will have a high positive value indicating a high degree of similarity. However, as Minkoff (1969) points out, the use of the correlation coefficient does require that all characters have the same directional properties. This condition is fulfilled when studies of resemblance are based on morphology and the forms are characterised by linear dimensions. It is in such studies that problems of size and shape resemblance arise and in which the normalising properties of the correlation coefficient are most welcome.

2.4.2 Distance coefficients

Several distance coefficients have been proposed as measures of similarity. One of the simplest of these is the Mean Character

Difference (MCD) whose use as a measure of taxonomic resemblance is discussed by Cain and Harrison (1958) and Huizinga (1962,1965). The MCD was first used by Czekanowski (1932), who called it the durchschnittliche Differenz. Related to this is the Mean Square Distance (and its square root) first used by Heincke (1898), the modern use of which as a measure of similarity is discussed by Penrose (1954), Sokal (1961) and Sokal and Sneath (1963).

These two coefficients are examples of a class of distance functions whose general formula is given by:

$$d_r(j,k) = \left(\sum_{i=1}^{n} \left| x_{ij} - x_{ik} \right|^r \right)^{1/r}$$

where x_{ij} is the value of character i for form j. In taxonomic use, the coefficient is usually multiplied by a factor $n^{-1/r}$ to take into account the fact that the number of characters used in a comparison may vary from comparison to comparison. If $r = 1$ then d_r is the so-called "city block" distance (see Fig. 2.1) and d_r/n is the Mean Character Difference. If $r = 2$ then d_r is the ordinary Euclidean distance and $d_r/\sqrt{n}$ is the square root of the Mean Square Distance. I know of no taxonomic use of d_r for $r > 2$. (A discussion of this class of distance functions is given by Kruskal, 1964).

The treatment of these two measures of resemblance as particular examples of a general formula is a useful reminder that there is no "true" distance between points in a character space. Although the Euclidean distance has an immediate intuitive

appeal it cannot, on this ground alone, be said to be superior to the MCD as a measure of taxonomic resemblance. For example, a taxonomist might feel that the Euclidean distance, since it is based on the sum of squared differences in character values, gives undue weight to large differences.

The MCD and the Mean Square Distance are measures of overall resemblance and give information about differences in both size and shape. The Mean Square Distance is, however, superior to the MCD in one respect since it is more easily partitioned into components which correspond with intuitive ideas of size and shape. Penrose (1954) defines the size of a form as the mean of its character values and the size distance between two forms as the square of the differences in their sizes. When this size distance is subtracted from the Mean Square Distance, a term remains which is the variance of differences between the character values of the forms being compared. Penrose suggests that this variance is a measure of the difference in shape between the two forms. However, as Rohlf and Sokal (1969) have pointed out, the shape coefficient is not a measure of similarity of proportions. It is zero, indicating identity of shape, only if the character values of one form are larger than those of the other by a constant amount. The normalising properties of the five coefficients considered here (cosine of the angle between the two forms, correlation coefficient,

Penrose's Shape coefficient, Mean Character Difference, Mean Square Distance) are summarised in the following table:

Coefficient	Normalises for: Proportional differences in size	Additive differences in size
Cosine	Yes	No
Correlation coefficient	Yes	Yes
Shape	No	Yes
MCD	No	No
MSD	No	No

The performance of these five measures of similarity is examined in more detail in Chapter 3.

2.5 The search for group structure

The inter-relationships among a very small number of forms can be studied by a direct examination of the similarity values. Or, if the object of the study is a comparison between a small number of forms and one form used as a standard, similarities can be represented by distances on a linear scale, with the reference form at one end. However, when the relationships among all forms are of interest, as they will be in the

construction of a classification, they cannot be shown on a linear scale and more complex methods of analysing the similarity values are needed. There are two reasons for this: first, the number of similarity values is usually considerably larger than the number of forms between which these values are calculated, since the number of comparisons (c) is related to the number of forms (t) by the formula:

$$c = \tfrac{1}{2}t(t - 1).$$

Secondly, the number of characters used in a comparison is usually greater than three and therefore the relationships between the forms and the clusters into which they fall cannot immediately be plotted on paper or shown in a solid model.

There are two main types of solution to the problem of analysing these multi-dimensional relationships, both of which are concerned with reducing the number of dimensions necessary to represent relationships. In terms of the geometrical model, clusters of points represent groups of similar forms and one type of solution attempts to delimit these clusters and to show them and their relationships on a simple two dimensional diagram. The second method seeks a projection of the points onto a space of fewer dimensions such that the distortion of relationships is minimised. The first solution, cluster analysis, is considered in Section 2.5.1 and the second, principal components analysis, in Section 2.5.2.

2.5.1 Cluster analysis

The methods of cluster analysis may conveniently be divided into two groups. Each sub-group in an hierarchical classification may be formed from the splitting into two parts of a larger group, or alternatively from the union of two smaller groups. These two types of methods have been called divisive and agglomerative (Macnaughton-Smith, Williams, Dale and Mockett, 1964). The disadvantage of divisive methods (such as, for example, that of Edwards and Cavalli-Sforza, 1965) is that they require very much more computation than do agglomerative methods. For example, 100 points can be split into 2 groups in approximately 10^{33} different ways. Each of these splits must be examined in order to determine which split produces the most homogeneous clusters. Some strategy is obviously needed in order to reduce the number of splits which must be examined. Such strategies are, however, difficult to devise and, up to now, most studies in quantitative taxonomy have been based on agglomerative methods. Only these are considered in this study.

Many different agglomerative clustering methods have been devised (for an extensive survey see Sokal and Sneath, 1963) but the methods most widely used in quantitative taxonomy are the group methods proposed by Sokal and Michener (1958). The basis of these methods is as follows: a table of similarity values is examined for groups of forms. A group is defined as

a set of forms which are more similar (in terms of a particular criterion) to each other than to the members of the other groups or to forms not included in groups. These "basic groups" form the nuclei of clusters and a new table of similarity values is calculated between different basic groups (each considered as a unit) and between them and forms not included in basic groups. This table of similarity values is in turn searched for basic groups. The process is repeated until only two units remain. The outcome is a branching diagram(dendrogram) which indicates the way in which the forms coalesce in groups (for example, Fig.3.2, p. 61). The similarity between any pair of groups is indicated by the level at which the stems from these join.

These methods may be subdivided into two types: variable- and pair-group methods. In the variable-group methods the groups produced at any stage in the clustering process can contain more than two members (a member is either one of the original forms or a group of forms produced in the preceding stage in the clustering process). The disadvantage of variable-group methods is that the taxonomist must decide, before clustering begins, on a level of similarity below which potential members are admitted to a group and above which they are excluded. In the pair-group methods, on the other hand, the groups produced at any particular stage in the clustering process

contain only two members. These groups are produced by placing together those units (which may be individual forms or groups of forms produced in a preceding stage in the clustering process) for which the relation "is most similar to" is reflexive. Olson and Miller (1958) have proposed the convenient name "basic pairs" for these groups.

In the time available for the study reported in this thesis, it was impossible to consider both variable- and pair-group methods. Since pair-group methods are easier to programme for computers than are variable-group methods, and since they are completely automatic they have been more frequently used in quantitative taxonomy. It seemed best, therefore, to concentrate attention on pair-group methods and in the discussion which follows and in the comparisons in Chapter 3 variable-group methods are not considered.

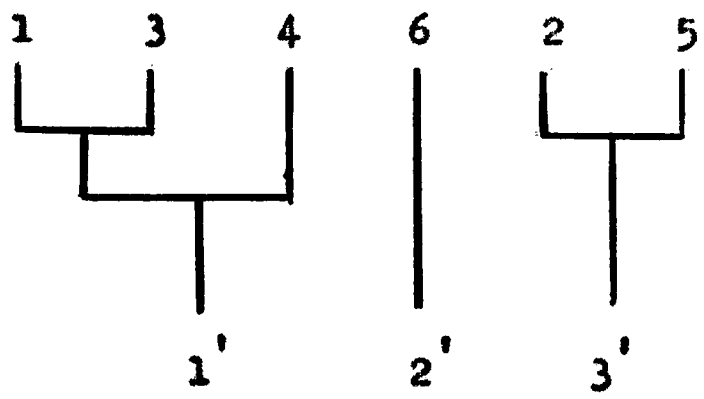
In the first stage of the clustering process, the units which link into basic pairs are the individual forms between which similarities have been measured. In order to calculate a new table of similarity values each of these pairs must be treated as if it were a single individual. The main problem which arises in the use of pair-group methods is that of deciding on a suitable definition of similarity between these basic pairs, considered as units, and between basic pairs and those individuals not yet in pairs. One solution to this problem,

discussed by Sokal and Sneath (1963), is to measure the similarity between two basic pairs by the arithmetic mean of the similarities between the individuals which make up the pairs. For example, the similarity (S) between a basic pair composed of forms 1 and 2 and a basic pair composed of forms 3 and 4 is:

$$S_{1+2,3+4} = \frac{1}{4}(S_{1,3} + S_{1,4} + S_{2,3} + S_{2,4})$$

where $S_{1,3}$ is the similarity between forms 1 and 3, $S_{1,4}$ the similarity between forms 1 and 4, etc.

After the first stage of the clustering process a new problem must be considered. The members of the basic pairs produced during a particular stage may be individual forms or they may be groups of forms linked together in a previous stage. The problem is this: should the method used to calculate similarity between the groups give equal weights to the individual forms within each group or should forms which entered early in the clustering process be given less weight than those which entered later? As an example, we suppose that a clustering of 6 forms has reached the following stage:



We wish to calculate the similarity between the three groups (1', 2', 3') in order to enter the next stage of the clustering process. Consider the similarity between the group 1' (forms 1, 3, 4) and group 2' (form 6): should the contribution of forms 1 and 3 to this similarity be equal to that of form 4, or should their <u>combined</u> contribution be equal to that of form 4? That is, should the similarity be given by:

$$S_{1+3+4,6} = \frac{1}{3}(S_{1,6} + S_{3,6} + S_{4,6})$$

or:

$$S_{1+3+4,6} = \frac{1}{2}(S_{4,6} + \frac{1}{2}(S_{1,6} + S_{3,6}))\ ?$$

The relative merits of these two approaches to the problem of delimiting clusters will be discussed in Chapter 3.

An alternative solution to the problem of measuring the similarity between groups of forms is suggested by the geometrical model described in Section 2.4. At any particular stage in the clustering process, the forms which have linked into groups may be thought of as clusters of points lying in a multi-dimensional space. The measure of similarity between two such groups proposed here is the distance between the centroids (the centres of gravity) of the clusters. The distance between the centroids (d_c) can be expressed in terms of the distances among the members of the two groups as follows:

$$d_c^2 = \overline{B} - \frac{t_1 - 1}{2t_1}\overline{W}_1 - \frac{t_2 - 1}{2t_2}\overline{W}_2$$

where $\overline{B}$ is the mean of the $t_1 t_2$ squared distances between the t_1 members of the first group and the t_2 members of the second, $\overline{W}_1$ is the mean of the $\frac{1}{2}t_1(t_1 - 1)$ squared distances among the members of the first group and $\overline{W}_2$ is the mean of the $\frac{1}{2}t_2(t_2 - 1)$ squared distances among members of the second group. For example, the distance between the centroid of a pair composed of forms 1 and 2 and the centroid of a pair composed of forms 3 and 4 is calculated as follows:

$$\overline{B} = \frac{1}{4}(d^2_{1,3} + d^2_{1,4} + d^2_{2,3} + d^2_{2,4})$$

$$\overline{W}_1 = d^2_{1,2}$$

$$\overline{W}_2 = d^2_{3,4}$$

$$d^2_c = \frac{1}{4}(d^2_{1,3} + d^2_{1,4} + d^2_{2,3} + d^2_{2,4}) - \frac{1}{4} d^2_{1,2} - \frac{1}{4} d^2_{3,4} .$$

In order to calculate the distance between the centroids of two clusters of forms it is necessary to know the distances among the individual forms which make up these clusters. However, the order in which these forms have linked together is not taken into account and the method is therefore similar to the first of the methods described above. It differs from this method in that the distance (= similarity) between two groups is a function not only of the average distance between the groups but also of the average distance within each group.

The clustering techniques based on simple averages are generally applicable to both types of coefficients of

similarity - angular and distance coefficients. The centroid method, however, can only be applied to coefficients which are in the form of distances (that is, coefficients which have the value zero when two forms are identical and which increase in magnitude as similarity decreases). In order to apply the centroid method to angular coefficients these must first be transformed to distances. The transformation used in this study is:

$$d^{s}_{jk} = 2\,(1 - a_{jk})$$

where a_{jk} is either the cosine of the angle or the correlation between forms j and k. A comparison between the centroid method and the two methods based on simple averages is made in Chapter 3.

2.3.2 Principal components analysis

An explanation of the taxonomic use of principal components analysis is simplified if the forms in which the taxonomist is interested are thought of as points in a multi-dimensional space. The inter-relationships of these points are described by a table of similarity values and principal components analysis uses the information in this table to refer the points to a new set of axes. These axes are chosen so that they are at right angles to each other and the first axis accounts for the greatest amount of variation among the points (i.e. the sum of

squares of projections of the points onto this axis is a maximum); the second axis accounts for as much as possible of the variation not accounted for by the first and so on. The points are plotted in a diagram or solid model with respect to the first two or three of these new axes and the pattern of inter-relationships of the forms is shown by the distribution of points. The distortion of the pattern of relationships produced by this reduction of dimensions depends upon the proportion of the total variation among the points accounted for by the first two or three of these new axes.

Sokal (1958) appears to have been the first to employ principal components analysis in the study of tables of similarity values. Sokal only applied the method to the analysis of tables of correlation coefficients but it is possible to use it in the analysis of any kind of similarity value although certain kinds, for example, distance coefficients, may need to be transformed first. This point is very clearly made by Gower (1965). Gower argues as follows*: suppose S is a symmetric matrix of similarity values of order t (an element s_{ij} of this matrix is the similarity between form i and form j) and let it have latent roots $l_1, l_2, \ldots, l_t$ with associated

---

* Gower's notation has been changed to that suggested by Sokal and Sneath (1963). The number of forms is thus represented by t and not n and the similarity between two forms by S_{ij} and not s_{ij}.

column vectors (the latent vectors) $\underline{c}_1, \underline{c}_2, \ldots, \underline{c}_t$. One may write down the vectors as a square array:

	Vector			
points	I	II	...	t
Q_1	c_{11}	c_{12}	...	c_{1t}
Q_2	c_{21}	c_{22}	...	c_{2t}
..	.	.	.	.
Q_t	c_{t1}	c_{t2}	...	c_{tt}
ROOT	l_1	l_2	...	l_t

where the r-th column is the vector $\underline{c}_r$. The technique outlined in the previous paragraph is to take the elements of the i-th row as the coordinates of a point Q_i in the t-space and the distance between Q_i and Q_j is then given by:

$$\overline{Q_iQ_j}^2 = \sum_{r=1}^{t} (c_{ir} - c_{jr})^2$$

$$= \sum_{r=1}^{t} c_{ir}^2 + \sum_{r=1}^{t} c_{jr}^2 - 2 \sum_{r=1}^{t} c_{ir}c_{jr} .$$

It is a property of latent vectors that if they are normalised so that their sums of squares are equal to their corresponding latent roots then:

$$\underline{S} = \underline{c}_1\underline{c}_1' + \underline{c}_2\underline{c}_2' + \ldots + \underline{c}_t\underline{c}_t' .$$

($\underline{c}_i'$ is the transpose of $\underline{c}_i$)

Consequently $S_{ii} = \sum_{r=1}^{t} c_{ir}^{2}$ and $S_{ij} = \sum_{r=1}^{t} c_{ir}c_{jr}$.

Therefore, if the vectors are normalised so that $\sum_{r=1}^{t} c_{ir}^{2} = l_r$ the distance between points Q_i and Q_j is given by:

$$\overline{Q_iQ_j}^2 = S_{ii} + S_{jj} - 2S_{ij}.$$

If $\underline{S}$ is a matrix of correlation coefficients then S_{ij} has the value +1 for complete identity between forms and the value -1 for forms which are complete opposites. Intermediate values correspond to different degrees of similarity. In this case the diagonal elements of $\underline{S}$ are unity and the distance between points Q_i and Q_j is given by:

$$\overline{Q_iQ_j}^2 = 2(1 - r_{jk}).$$

Thus for identical forms ($r_{jk} = +1$) Q_i and Q_j coincide; with complete disagreement ($r_{jk} = -1$) the points Q_i and Q_j are separated by the maximum possible distance. The points therefore have the right sort of metric properties for representing the inter-relationships of the forms.

If a principal components analysis is carried out on a table of distance values one or more of the latent roots may be negative (Gower, 1965) and, if so, one or more of the coordinate axes will be imaginary. It will thus be impossible to construct a diagram or model showing the relationships of

the forms. A suitable transformation to overcome this difficulty is:

$$S_{ij} = 1 - kd_{ij}^2$$

where d_{ij} is the distance (measured by an appropriate distance coefficient) between form i and form j; k is a factor chosen to ensure that S_{ij} is never negative.

The justification for this transformation is as follows: the distance between points Q_i and Q_j is related to the similarity between forms i and j by the expression:

$$\overline{Q_i Q_j}^2 = S_{ii} + S_{jj} - 2S_{ij} .$$

If we consider the similarity between two forms to be the transformed distance between them and substitute for S_{ii}, S_{jj} and S_{ij} in the above formula (remembering that the distance between a form and itself is zero and therefore S_{ii} and S_{jj} equal one) we find that the distance between points Q_i and Q_j is given by:

$$\overline{Q_i Q_j}^2 = 1 + 1 - 2(1 - kd_{ij}^2)$$

$$= 2kd_{ij}^2$$

The distance between the points Q_i and Q_j will therefore represent the distance between the forms i and j.

It must be emphasised that an exact representation

of the relationships between forms can be obtained only by using all latent vectors. A good representation in a reduced number of dimensions will only be obtained if some latent roots are small. If a latent root l_r is small then the contribution $(c_{ir} - c_{jr})^2$ to the distance between Q_i and Q_j will be small. The relative values of the latent roots are determined by the distribution of forms in the character space. If certain parts of the character space are sparsely filled, as will be the case if the forms studied fall into clusters, then certain of the latent roots will have much smaller values than others. This topic is considered in more detail in the next section.

A general discussion of principal components analysis is given by Rao (1964).

2.6 Relationship between Q and R techniques

The methods discussed in the previous section operate upon tables of similarities between forms. An alternative approach is to analyse the relationships between the characters used to describe the forms. Those techniques which analyse tables of similarities between forms are known as Q techniques and those which analyse relationships between characters as R techniques (Sokal and Sneath, 1963, p.124).

One of the needs of quantitative taxonomy is an investigation of the relationships between the two kinds of technique. A detailed investigation is not attempted here but some aspects of the relationships will be discussed.

When considering R techniques it is important to distinguish two situations. In the first, the units of classification are individual forms about which no prior judgments are made, whereas, in the second, the units of classification represent groups of forms which are defined before classification begins. For example, the groups may be species recognised by breeding criteria and the individuals within each species represented by a mean vector whose elements are character means. In the second situation, the relationships between characters can be studied both between and within the groups.

The former situation is found in many classificatory studies and the R techniques which are discussed first are those which apply to this situation. In discussing these techniques it is convenient to think of the relationships between forms in geometric terms. The character values for each form are regarded as the coordinates of points with respect to a number of orthogonal axes, one for each character used to describe the forms. If the distribution of points within

this character space is not uniform, the values of certain characters will vary together. This association is conveniently measured by means of the covariance or the correlation between pairs of characters.

Since the covariation of characters is the result of the non-uniform distribution of points in the character space, information about the distribution may be obtained by analysing the table of covariances between characters. For example, Rao (1964) shows that the problem of projecting the points into a space of reduced dimensions with the minimum of distortion may be solved by using the latent vectors of the covariance table. These may be regarded as new axes, the first of which lies in the direction of maximum dispersion of the points, the second in the direction of maximum dispersion of points perpendicular to the first axis and so on. The elements of a vector are the cosines of the angles between it and the original character axes. The projections of the points onto these new axes are obtained by multiplying the character values for a form by the corresponding elements in the vector and adding the products.

The purpose of this analysis is thus the same as that of a Q-type principal components analysis of tables of similarities between forms. What is the relationship between the two approaches? This will depend upon the particular

methods used to measure covariation of characters and similarity between forms. Gower (1965) points out that for certain pairs of R and Q techniques the results are identical. He shows, for example, that the projections of points obtained from the latent vectors of a table of correlations between characters are the same as those obtained by a principal components analysis of distances between forms when these are based on standardised character values (and providing the data do not contain any missing values). The relationships between forms may therefore be studied by either method.

Since the number of characters is usually much larger than the number of forms, a principal components analysis of correlations between characters involves more computation than one of similarities between forms. The results of the R approach, however, provide more information than do those of the Q approach. The results of the latter are simply the projections of points onto new axes whereas an R analysis gives not only these projections but also the directions of the new axes with respect to the original character axes. The relative importance of the original characters in determining the dispersion of forms in the character space may therefore be determined by comparing their directions with those of the latent vectors. For example, the first latent

vector lies in the direction of maximum dispersion of the forms and therefore those characters which lie in directions similar to that of the first vector are the characters which contribute most to the dispersion of forms. A study of the relative importance of characters is helpful in two ways. It shows which character or characters are most useful for discriminating between groups of forms and thus helps in the construction of keys. It may also provide valuable information with which to recognise functional and morphological trends. Since such trends are likely to represent single phyletic lineages or groups of closely related lineages (Harrison and Weiner, 1964) their recognition is an aid in determining the phyletic relationships of the forms.

When the units of classification represent groups of forms recognised before classification begins it is possible to take into account the covariation of characters within each group when studying relationships between the groups. If the patterns of character covariation are the same within each group, the groups may be represented by points in space defined by oblique character axes. The angle between any pair of axes is determined by the covariance of the corresponding characters within the groups. The distance between groups i and j which corresponds to the Euclidean distance in a space defined by

orthogonal axes is given by:

$$D^2_{ij} = (\underline{X}_i - \underline{X}_j)' \underline{W}^{-1} (\underline{X}_i - \underline{X}_j)$$

where $\underline{X}_i$, $\underline{X}_j$ are the column vectors of character means for groups i and j and $\underline{W}^{-1}$ is the inverse of the within group character covariance matrix. Mahalanobis (1930, 1936) has suggested that the resemblance between groups be measured by this distance and Rao (1952, 1964) has shown that the representation of points in a space of q dimensions which best preserves these distances is obtained by projecting the groups into a space defined by the first q latent vectors $\underline{c}_i$ which are the solutions of the equation:

$$(\underline{B} - \lambda \underline{W})\underline{c} = \underline{0}$$

where $\underline{B}$ and $\underline{W}$ are the covariance matrices between and within the groups and λ the latent roots corresponding to the latent vectors. The vectors are usually referred to as Canonical Variates and the method of analysis as Canonical Analysis.

Although the measurement of resemblance by Mahalanobis's Distance and the use of Canonical Analysis as a means of studying these distances have proved useful techniques in a number of taxonomic studies (for examples, see Blackith, 1965) their application is only justified when the within group covariances can be assumed to be identical. In many taxonomic situations this assumption is likely to be false. When the

units of classification are biological species, the covariation of characters reflects the adaptation of the species to its particular ecological niche. Species occupying different ecological niches will therefore show different patterns of character covariation and the use of the above technique to investigate their resemblance is therefore unjustified. Measures of resemblance which take into account differences in character covariation within groups have been proposed (for example, by Rao, 1948 and Reyment, 1962) but their general taxonomic use remains to be investigated.

2.7 Summary

The purpose of this chapter has been to discuss some of the problems which face the taxonomist when he wishes to use quantitative methods to investigate taxonomic relationships.

The first stage in the use of quantitative methods involves the choice of forms and characters to describe these forms. The forms are the units of classification and are of many different kinds. Their choice is determined simply by the interests of the taxonomist. It is important to distinguish units about which no previous judgments are made from units which are chosen from groups previously defined. In the second case, it is necessary to consider the degree to which the units represent the groups from which they are chosen.

A taxonomic character is anything which may be considered as a variable independent of any other thing considered at the same time. Measures of overall resemblance should be based on as many characters as possible but characters which do not vary over the forms considered may be ignored. A functional approach to the definition of morphological characters increases the information content of measures of resemblance.

The second stage involves the transformation of character values. Transformation is necessary when characters are measured in different units but may also be used when characters are measured in the same unit to increase the sensitivity of measures of similarity to particular components of resemblance.

The third stage involves the choice of similarity coefficient. The particular coefficients considered here may be divided into angular and distance coefficients and the representation of forms by points in a multi-dimensional character space helps in the interpretation of these coefficients. Both angular and distance coefficients are valid measures of resemblance. When based on morphological characters they show different degrees of sensitivity to the size component of resemblance. Angular coefficients are less sensitive than distance coefficients to differences in size.

The fourth stage involves the analysis of tables of similarity values in order to express the multi-dimensional

relationships of the units of classification in a more easily understood form. Two groups of methods are considered here. Cluster analysis delimits the groups into which the units fall and shows these groups and their inter-relationships in a simple two-dimensional diagram. The methods of cluster analysis differ mainly in the way in which they define similarity between the groups and in the relative weight they give the members of these groups. Principal components analysis projects the units into a space of reduced dimensions with the minimum distortion of relationships. It can be applied to both angular and distance coefficients. A projection into a space of reduced dimensions may also be obtained by a principalcomponents analysis of the covariances between the characters used to describe the units. This analysis also indicates the degree to which different characters determine the distribution of the units in the character space.

These stages result in a quantitative picture of the phonetic relationships of the units studied. The inter-connections of these stages may be summarized by means of a diagram. This is shown in Fig. 2.2. It should be noted that this diagram is not intended to suggest that the information provided by the quantitative methods is necessarily sufficient to determine the phyletic relationships of the units of classification.

Figure 2.2

Inter-connections of the stages in the quantitative analysis of taxonomic relationships. The number on a stage indicates the section in Chapter 2 in which it is discussed

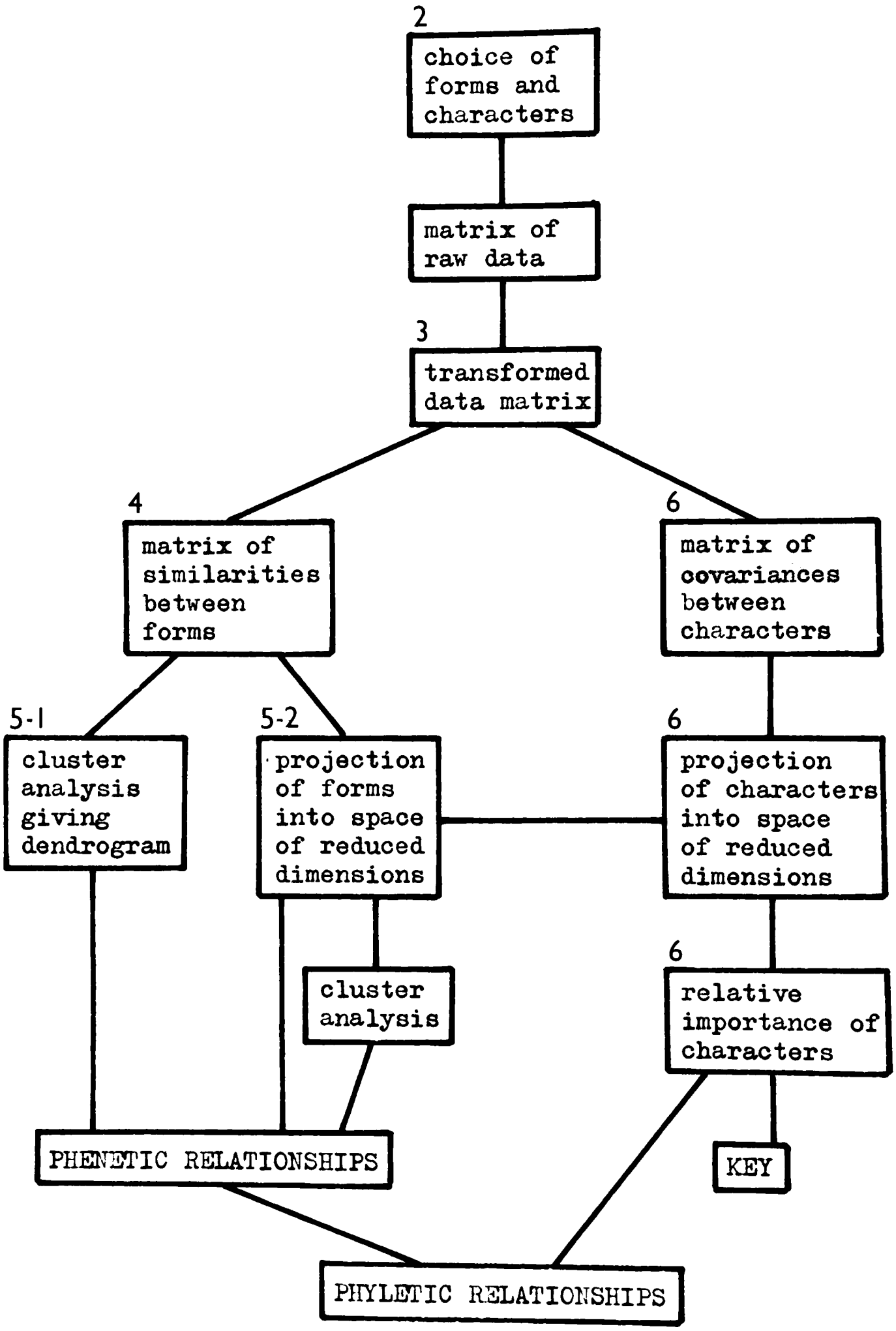

2
choice of forms and characters
matrix of raw data
3
transformed data matrix
4
matrix of similarities between forms
6
matrix of covariances between characters
5-1
cluster analysis giving dendrogram
5-2
projection of forms into space of reduced dimensions
6
projection of characters into space of reduced dimensions
cluster analysis
6
relative importance of characters
PHENETIC RELATIONSHIPS
KEY
PHYLETIC RELATIONSHIPS

TABLE 2.1

FORMULAE USED IN CALCULATING MEASURES OF SIMILARITY

---

1 Notation : X_{ij} is the value of character i for form j

n is the number of characters used in a particular comparison

t is the number of forms being compared

2 Mean of character i :

$$\bar{X}_i = \frac{1}{t} \sum_{j=1}^{t} X_{ij}$$

3 Standard deviation (s_i) of character i :

$$s_i^2 = \frac{1}{t-1} \left(\sum_{j=1}^{t} X_{ij}^2 - \frac{1}{t} \left(\sum_{j=1}^{t} X_{ij} \right)^2 \right)$$

4 Transformed character values :

$$X'_{ij} = (X_{ij} - \bar{X}_i) / s_i$$

5 Cosine of angle :

$$\cos \theta_{jk} = \frac{\sum_{i=1}^{n} X_{ij} X_{ik}}{\left(\sum_{i=1}^{n} X_{ij}^2 \right)^{\frac{1}{2}} \left(\sum_{i=1}^{n} X_{ik}^2 \right)^{\frac{1}{2}}}$$

TABLE 2.1— Continued

6 Correlation Coefficient :

$$r_{jk} = \frac{\sum_{i=1}^{n} x_{ij}x_{ik} - \frac{1}{n}\left(\sum_{i=1}^{n} x_{ij}\right)\left(\sum_{i=1}^{n} x_{ik}\right)}{\left(\sum_{i=1}^{n} x_{ij}^2 - \frac{1}{n}\left(\sum_{i=1}^{n} x_{ij}\right)^2\right)^{\frac{1}{2}}\left(\sum_{i=1}^{n} x_{ik}^2 - \frac{1}{n}\left(\sum_{i=1}^{n} x_{ik}\right)^2\right)^{\frac{1}{2}}}$$

7 Mean Character Difference (MCD) :

$$MCD_{jk} = \frac{1}{n}\sum_{i=1}^{n}\left|x_{ij} - x_{ik}\right|$$

8 Mean Square Distance (MSD) :

$$d_{jk}^2 = \frac{1}{n}\left(\sum_{i=1}^{n} x_{ij}^2 + \sum_{i=1}^{n} x_{ik}^2 - 2\sum_{i=1}^{n} x_{ij}x_{ik}\right)$$

9 Size difference :

$$Q_{jk}^2 = \frac{1}{n^2}\left(\sum_{i=1}^{n} x_{ij} - \sum_{i=1}^{n} x_{ik}\right)^2$$

10 Shape difference :

$$Z_{jk}^2 = \frac{n}{n-1}\left(d_{jk}^2 - Q_{jk}^2\right)$$

3 COMPARISONS BETWEEN THE METHODS

3.1 Introduction

Some of the problems which the taxonomist has to face when he wishes to study phenetic affinity between organisms were considered in Chapter 2. These problems fall into three main groups: those connected with the selection of forms and the selection and transformation of characters, with the choice of similarity coefficient, and with the analysis of tables of similarity values. In this chapter, some of the different solutions to these problems are compared in action, using as the basis for the comparisons measurements made on the skulls of a number of hominoid Primates. The purpose of this introduction is to discuss the problem of evaluating different methods and to decide upon the best order in which to consider the problems.

When different methods give different results, the taxonomist must decide upon criteria by which to judge the relative merits of the different methods. What kinds of criteria can he use? The answer to this question will depend upon the purposes for which he is carrying out the study and upon the particular class of methods he is considering. For instance, the criteria used to judge between similarity

coefficients will not necessarily be the same as those used to judge between methods of analysing tables of similarity values.

The particular purpose of the taxonomist considered here is that of investigating phenetic relationships in quantitative terms. By this is meant the measurement of overall resemblance between forms and the construction of groups the members of which show a high degree of overall resemblance to one another. The concept of "overall resemblance" is, however, a vague one - the taxonomist does not know the "true" overall resemblance between forms and so cannot use this as a criterion with which to judge the relative merits of different methods. The particular approach adopted here is to take a well known group of forms and to ask the following questions: do the quantitative estimates of similarity between forms correspond with intuitive ideas of the overall resemblance between the forms; are certain methods more sensitive than others to the effects of factors such as size, age and sex which the taxonomist may wish to ignore when studying overall resemblance; do the patterns of relationships revealed by the various methods correspond with each other and those recognised by traditional methods?

The effects of a particular transformation of character values are most easily studied by comparing the pattern of

relationships based on transformed character values with that based on untransformed character values. In order to eliminate the effects of different coefficients of similarity this comparison should be based on a single coefficient. The choice of a suitable similarity coefficient must therefore be considered first. However, in order to study the information about relationships provided by a particular kind of similarity coefficient some method of condensing a table of similarity values into an easily understood form is needed. It is necessary, therefore, to consider the different stages in the construction of a phenetic classification in an order which is the reverse of that employed by the taxonomist.

In the following sections, the methods of analysing tables of similarity values are compared first, this comparison is followed by a comparison of different coefficients of similarity using one particular method of cluster analysis in order to condense the tables into an easily understood form. The effect of transformation of character values is then considered. Finally, the results of the comparative studies are briefly summarised.

3.2 The material used in making the comparisons

In order to compare the relative merits of the methods and the kinds of taxonomic information they produce, the

relationships of four groups of hominoids were studied. These were the three genera of large apes (Pongidae)* and modern Homo sapiens. These groups were considered to be well-defined, that is the variation within each group is much less than that between each group and therefore each may be represented by only a single form. However,a male, female and juvenile from each group were included in the analysis in order to study the reaction of the methods to two sources of variation, differences in sex and age, which the taxonomist may wish to ignore when constructing a phenetic classification. In addition, several fossil forms were included to allow comparisons to be made between the patterns of relationships of the fossil forms (with each other and with the four modern groups) revealed by the different methods.

Only the skulls of these forms were considered in this study since these were thought to provide sufficient information about the phenetic relationships of the four main groups to allow meaningful comparisons to be made between the different methods. Measurements of similarity between several of the fossil forms were necessarily based on their skulls because of a lack of known post-cranial material. The twenty skulls used in this analysis are listed

---

* Pan (chimpanzees), Pongo (orang-utans), and Gorilla (gorillas)

in Table 3.1. The fossil skulls were chosen to sample each of the main stages leading to modern Homo sapiens : the Australopithecine stage was represented by a cast of the infant skull from Taung, a cast of an almost complete skull from Sterkfontein ("Plesianthropus") and a cast of a skull from Swartkrans ("Paranthropus"). The pithecanthropine stage was represented by a cast of the skull of Pekin man (a reconstruction by Weidenreich based on skulls from Choukoutien) and the Hominine stage by casts of skulls from Broken Hill (Rhodesian man), La Chapelle aux Saints, Mount Carmel (skull number 5 from the Skuhl cave) and Steinheim. Each skull was given a reference number, this appears in the right-hand column of Table 3.1.

Further details of the fossil skulls and of the sites at which they were found are given in Day (1965).

3.3 The characters on which the comparisons were based

The problem of the choice of characters was considered in Section 2.2. Several criteria which can guide the taxonomist in his choice of characters and help him to determine the number on which to base comparisons were established. The first criterion is that the choice of characters should be

as wide as possible in order that the estimates of similarity reflect overall resemblance. The second is that characters which do not vary over the forms considered are of no importance for the purpose of measuring overall resemblance since the information they provide is redundant and their inclusion simply reduces the sensitivity of the measurements of similarity. The third criterion is that characters should, in the case of a structure such as the mammalian skeleton, be defined with respect to function.

These three criteria were used in choosing characters to provide data with which to compare the methods. The skull was divided into fourteen functional areas and characters were sampled from each. The functional areas and the number of characters from each are listed in Table 3.2. An attempt was made to characterise those aspects within each functional area which varied over the forms considered, and 99 characters were needed to do this. These characters are listed in Table 3.3. Most characters were linear dimensions expressed in millimetres and these were measured by means of calipers. Certain characters were measured on the surface of the skull by means of a steel tape. Some parts of the skull could not easily be expressed in terms of linear dimensions (for example, the elevation of the nasal bones and the development of the nasal sill and spine) and were instead divided into states

numbered according to the degree of development of the parts. Finally, certain characters (for example, those describing the shape of the mandibular symphysis) were angles measured in degrees. The method of measuring each character is noted in the list of characters (Table 3.3).

The character values for the hominoid skulls are listed in Table 3.4. The skull numbers refer to those given in Table 3.2 and the character numbers to those given in Table 3.3.

3.4 Methods of analysing tables of similarity values

In sections 2.5 and 2.6 the problem of expressing the multi-dimensional relationships of forms in an easily understood way was considered. The solutions to this problem were divided into two groups: cluster analysis and principal components analysis. In this section the performance of methods from both groups is studied. The methods were applied to tables of similarities based on standardised character values. That is, the values were transformed so that their mean became the origin and their standard deviation the unit of measurement. Similarity values were calculated between each pair of forms and since 20 forms were used 190 comparisons were made. (see Table 3.8).

3.4.1 Cluster analysis

Several methods of cluster analysis were discussed in Section 2.5.1 and a distinction was made between variable-

and pair-group methods. The pair-group methods were considered to be superior to variable-group methods on the grounds that they do not require an arbitrary criterion of group formation. Pair-group methods were divided into two groups - those which give equal weight to the members of groups when determining the similarity between groups (usually called unweighted methods) and those which give greater weight to forms which enter groups late in the clustering process (usually called weighted methods). A further distinction was made between unweighted methods which use the average similarity between the members of two groups as a measure of the similarity between the groups and those which use the distance between the centroids of two groups as a measure of similarity. The three methods compared here are the weighted pair-group method using averages (WPGMA), the unweighted pair-group method using averages (UPGMA) and the unweighted pair-group method using distances between centroids (UPGMC). The methods are applied to tables of correlation coefficients and tables of mean square distances.

The results of the methods are expressed in the form of dendrograms which indicate the way in which the forms coalesce in pairs. The similarity between any two groups of forms is indicated on the scale at the bottom by the level at which the stems from these join. It must be emphasised, though, that

the stems may be rotated through 180° and the order of forms in the right-hand column is to this extent arbitrary. The convention adopted here is to identify each group as it is formed in the clustering process by its lowest numbered member and to arrange the stems so that low-numbered groups are above high-numbered ones, except in cases where another order helps to emphasise certain features of the dendrogram.

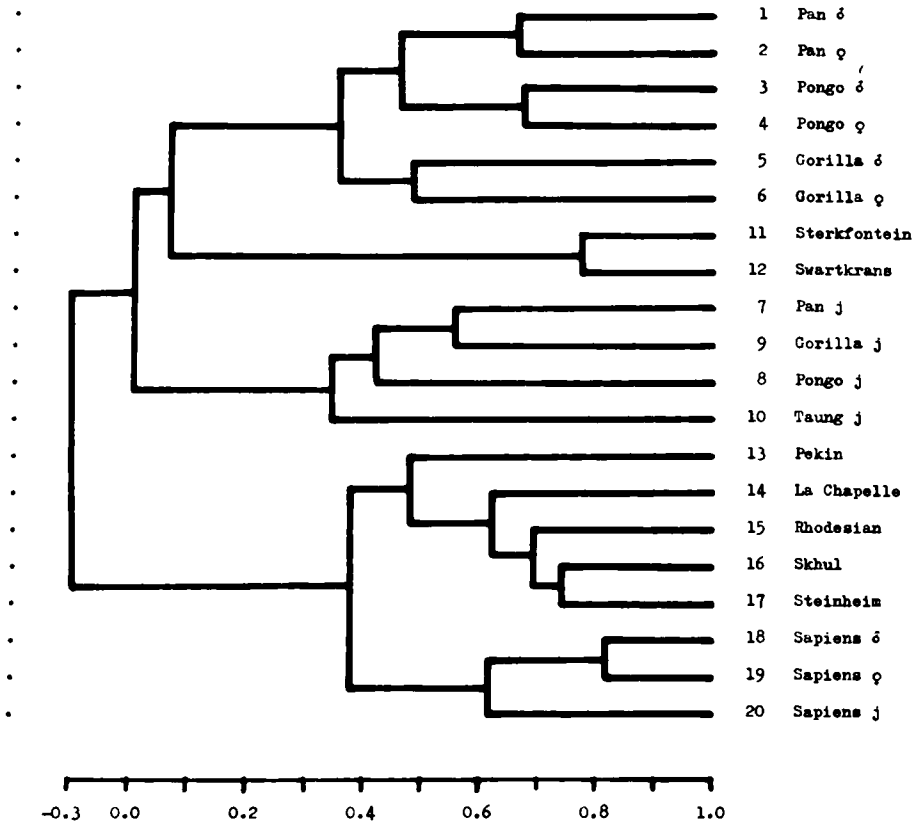
Fig. 3.1 shows the results of applying the two unweighted pair-group methods to a table of correlations between forms. Fig. 3.1 (a) is based on the average method and Fig. 3.1 (b) is based on the centroid method. The most obvious characteristic of the two dendrograms is the emphatic way in which the relationships are shown. Both diagrams indicate that the twenty forms fall into two main groups, the first of which consists of the adult and juvenile apes and the Australopithecines (forms 1 - 12) and the second consists of the fossil and modern hominids (forms 13 - 20). Within the first group, there is a division into three subgroups - the adult apes, the juvenile apes (with the juvenile from Taung) and the adult Australopithecines. Within the hominid group there is a division into modern and fossil forms.

The overall pattern of relationships produced by the average method is thus very similar to that produced by the

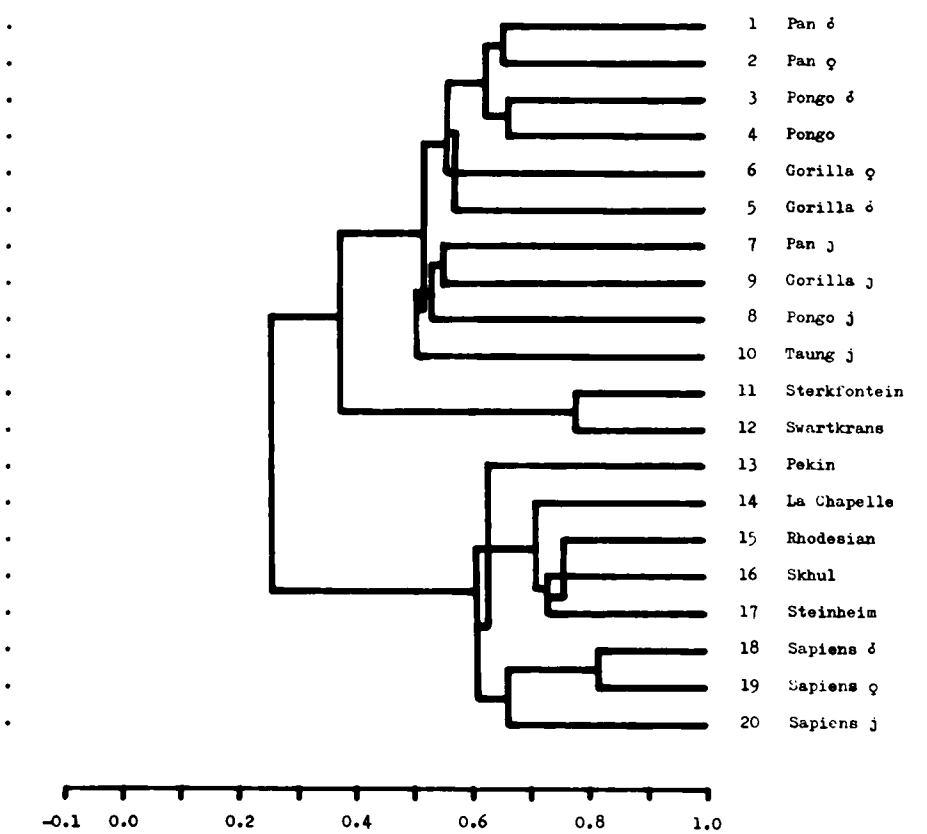
Figure 3.1

Comparison between average and centroid methods of cluster analysis. (a) Dendrogram produced by unweighted pair-group method using averages. (b) Dendrogram produced by unweighted pair-group method using distance between centroids.

Dendrograms based on correlations between hominoid skulls calculated from standardised character values. The correlation between any two joining stems can be found by reading the value on the scale corresponding to the vertical line connecting the stems.


1 Pan ♂
2 Pan ♀
3 Pongo ♂
4 Pongo ♀
5 Gorilla ♂
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
-0.3 0.0 0.2 0.4 0.6 0.8 1.0

a


1 Pan ♂
2 Pan ♀
3 Pongo ♂
4 Pongo
6 Gorilla ♀
5 Gorilla ♂
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
11 Sterkfontein
12 Swartkrans
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
-0.1 0.0 0.2 0.4 0.6 0.8 1.0

b

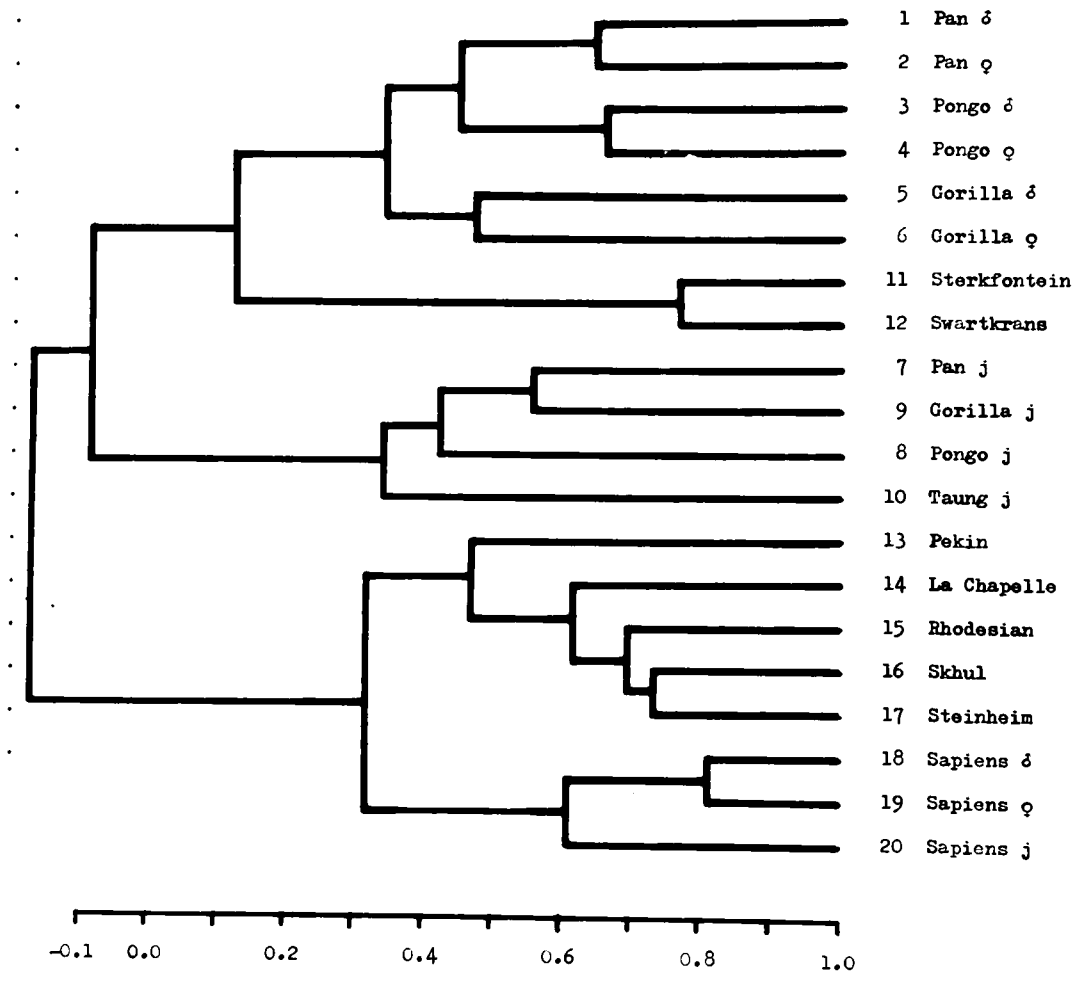
centroid method but there are a number of differences in detail. One obvious difference is that in the dendrogram produced by the average method the adult apes link first with the adult Australopithecines while in the dendrogram produced by the centroid method the adult apes link first with the juvenile apes (including the Australopithecine from Taung) and then with the adult Australopithecines. A second difference is that in the average method, as the groups link up, their average similarity always decreases while in the centroid method the distance between centroids sometimes decreases (and hence the similarity between groups increases). This will occur when two potential members of a group are on the same side of the group. If one member links with the group to form a basic pair, the centroid of the new group will move towards the second candidate. If this in turn links with the new group to form a basic pair a "reversal" will be shown on the dendrogram.

In addition to giving a slightly different picture the centroid method produces very much "tighter" clusters than does the average method.

The second comparison made here is between the weighted and unweighted pair-group methods. Fig 3.2 shows the result of applying the weighted method to a table of correlations between forms. A comparison of this with Fig. 3.1 (a) shows

Figure 3.2

Dendrogram produced by weighted pair-group cluster analysis of correlations calculated from standardised character values.

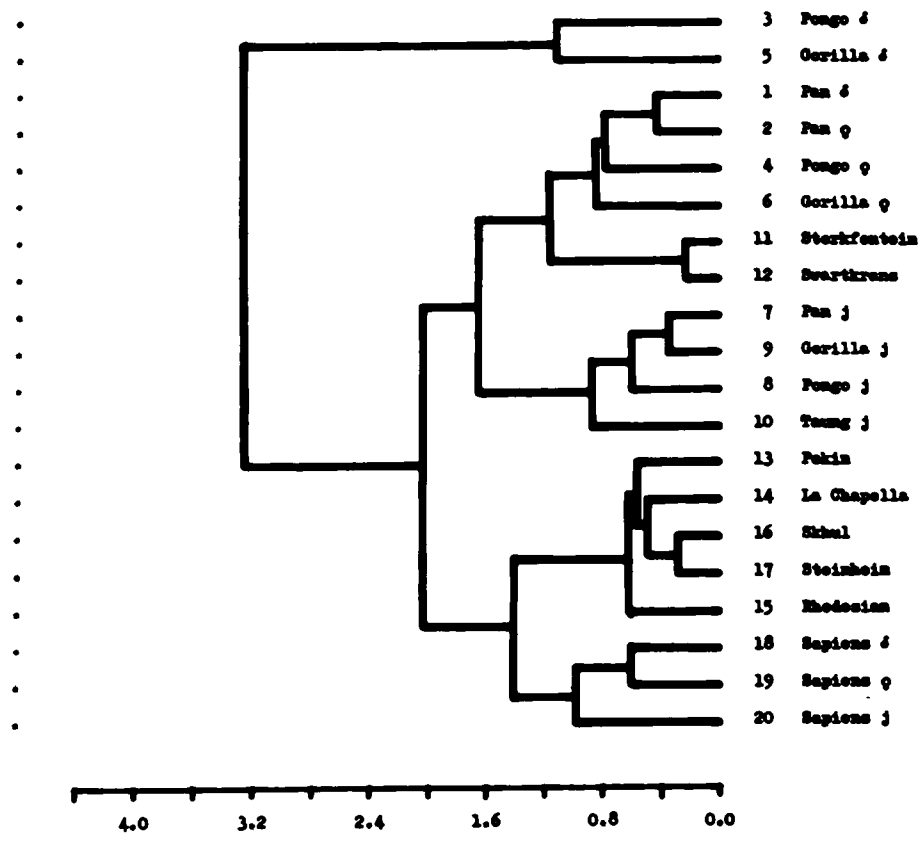

1 Pan ♂
2 Pan ♀
3 Pongo ♂
4 Pongo ♀
5 Gorilla ♂
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
-0.1
0.0
0.2
0.4
0.6
0.8
1.0

that there is no difference between the patterns of relationships produced by weighted and unweighted methods although the levels at which corresponding stems join do differ. However, when weighted and unweighted methods are applied to a table of Mean Square Distances between forms (based on the same character values as the correlations) differences in outcome do appear. Fig. 3.3 (a) is a dendrogram produced by the unweighted method and Fig. 3.3 (b) is a dendrogram produced by the weighted method. The most striking difference between the two dendrograms is in the relative positions of the fossil hominids and the juvenile apes. In the dendrogram produced by the unweighted method the group of fossil hominids (forms 13 - 17) links with the modern Homo sapiens group (forms 18 - 20) and the group of juvenile apes and Taung (forms 7 - 10) links with the group of adult apes (excluding the adult gorilla and orang) and adult Australopithecines (forms 1, 2, 4, 6, 11, 12). In the dendrogram based on the weighted method, however, the pattern is reversed: the group of juvenile apes and Taung links with the modern Homo sapiens group while the group of fossil hominids links with the group of adult apes and adult Australopithecines. The explanation of this difference lies in the relative weights given to the members of these

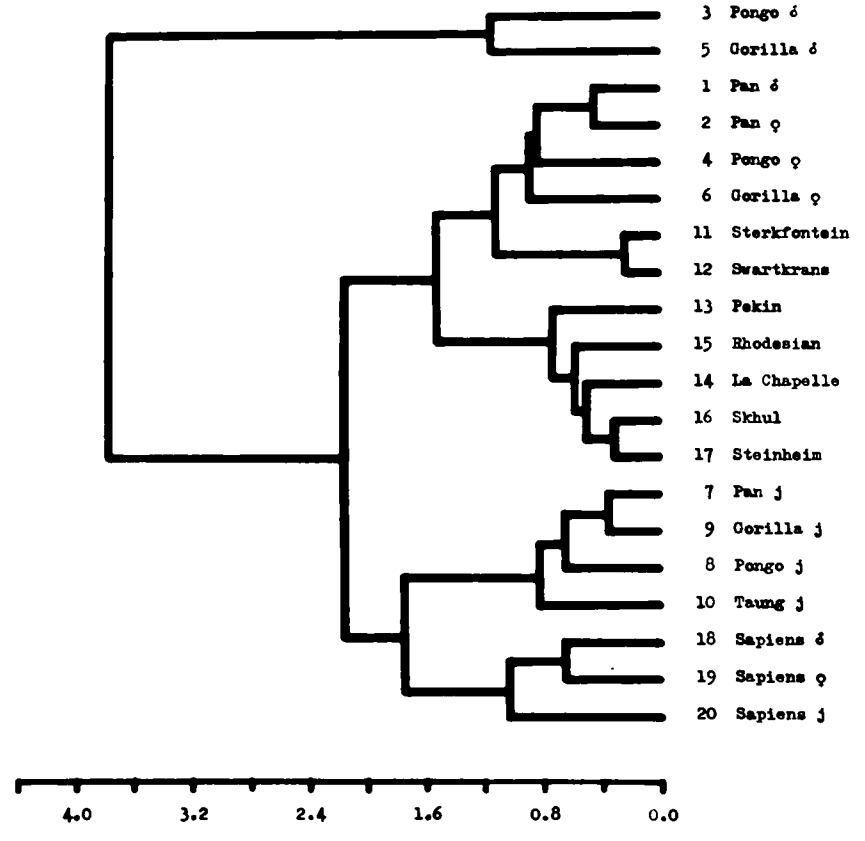
Figure 3.3

Comparison between unweighted and weighted methods of cluster analysis. (a) Dendrogram produced by unweighted pair-group method. (b) Dendrogram produced by weighted pair-group method. Both dendrograms use averages to measure similarity between groups.

Dendrograms based on mean square distances calculated from standardised character values.


3 Pongo ♂
5 Gorilla ♂
1 Pan ♂
2 Pan ♀
4 Pongo ♀
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
16 Skhul
17 Steinheim
15 Rhodesian
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
4.0
3.2
2.4
1.6
0.8
0.0

a


3 Pongo ♂
5 Gorilla ♂
1 Pan ♂
2 Pan ♀
4 Pongo ♀
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
13 Pekin
15 Rhodesian
14 La Chapelle
16 Skhul
17 Steinheim
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
4.0
3.2
2.4
1.6
0.8
0.0

b

groups by the weighted and unweighted methods.

In the weighted method, the similarity between two groups is the weighted average of the similarities between the members of the groups. If $S_{A,B}$ is the similarity between groups A and B then:

$$S_{A,B} = \sum_{ij} w_i w_j S_{ij} \Big/ \sum_{ij} w_i w_j$$

where S_{ij} is the similarity between the i-th member of group A and the j-th member of group B, w_i is the weight given to the i-th member of group A and w_j the weight given to the j-th member of group B. These weights are determined as follows: unit weights are given to the pair of individuals which form the nucleus of the group; the other members of the group are considered in the order in which they link to this nucleus and each form is given a weight equal to the combined weights of those forms which linked to the nucleus before it. For example, in Fig. 3.3 (b), the nucleus of the fossil hominid group is the pair of forms 16-17 and these are given unit weights. The next form to link is 14 and this is given weight 2 ($= w_{16} + w_{17}$); form 15 links next and is given weight 4 ($= w_{14} + w_{16} + w_{17}$); finally, form 13 links and is given weight 8.

A part of the cluster analysis which produced the dendrograms of Fig. 3.3 is shown in Table 3.5. This shows the calculation of the weighted and unweighted similarity between the fossil hominid group and the modern Homo sapiens group. S is the

weighted similarity and S' is the unweighted similarity between the two groups (S' is simply the mean of the 15 S_{ij} values). The effect of using weights is clearly shown in this table: the distances between forms 13 and 20 and forms 15 and 20 are greatly increased relative to the other distances.

When the similarity between the fossil hominid group and the ape-adult Australopithecine group is calculated, the unweighted similarity is found to be 1.555 and the weighted similarity 1.51[illegible]. In geometric terms the hominid group may be thought of as approximately equidistant from the other two groups. The "outliers" of the hominid group (forms 13 and 15) are closer to those of the ape-Australopithecine group (forms 11 and 12) than to that of the Homo sapiens group (form 20) and the greater weight attached to these outliers in the weighted method is sufficient to link the fossil hominid group to the ape-Australopithecine group and so produce a pattern of relationships which is the reverse of that shown by the unweighted method. When similarity is measured by means of the correlation coefficient the fossil hominid group is much closer to the modern Homo sapiens group than to the ape-Australopithecine group and the two methods give identical results.

The three methods of cluster analysis compared here thus give slightly different pictures of the relationships between the forms. The problem now considered is: is it possible to

measure the degree of concordance between the dendrograms produced by different methods and between the dendrograms and the table of similarity values on which they are based? The technique used here is a modification of the method of "cophenetic correlations" devoloped by Sokal and Rohlf (1962). They measured the concordance between a table of similarity values and a dendrogram by the correlation between the similarity values and "cophenetic" values extracted from the dendrogram. Sokal and Rohlf divided the similarity values along the side of the dendrogram into a number of equal intervals by drawing lines as class limits across the dendrogram and defined the cophenetic value of two forms as the class mark of the class in which their stems connected. The technique used here defines the cophenetic value of two forms as the actual similarity value at which the stems from them join. Cophenetic values between all pairs of forms are calculated and the values obtained are compared with the similarity values on which the dendrogram is based or with cophenetic values obtained from another dendrogram. The concordance is measured by the product-moment correlation coefficient.

The cophenetic correlations obtained by applying this technique to the three dendrograms based on the table of

correlations between the forms are shown below:

	r	WPGMA	UPGMA	UPGMC
r	-	0.861	0.890	0.869
WPGMA		-	0.982	0.898
UPGMA			-	0.959
UPGMC				-

The abbreviations are those used on p. 57; r denotes the original table of correlations between forms on which the dendrograms are based.

Inspection of the table shows that in general the correlations between the dendrograms and the original correlation coefficients are high. Of the three methods the unweighted pair-group method using averages (UPGMA) has the highest correlation with the original correlations and so may be said to reproduce the pattern of relationships most faithfully. The two unweighted methods show higher correlations than does the weighted method. The similarity between the dendrograms produced by the weighted and unweighted average methods has already been pointed out. The high correlation between the dendrograms (0.982) confirms the result of the previous comparison.

Sokal and Rohlf (1962) compared four methods of cluster analysis: two variable-group methods and two pair-group methods. The pair-group methods were both weighted methods -

one expressed the similarity between the groups by Spearman's sums of variables method (see Sokal and Sneath, 1963, p.183), the other by the average similarity between the members of the groups. This second method is the same as the weighted method considered here. Sokal and Rohlf found that of the four methods, the weighted method using averages gave the highest correlation with the original similarity values. They found a correlation of 0.86 for this method (this happens to agree with the correlation for this method in this study). Unfortunately, since Sokal and Rohlf did not consider any unweighted pair-group methods further comparisons between their results and those obtained here cannot be made.

The main conclusions which can be drawn from this comparative study of three pair-group methods of cluster analysis are as follows:

1. The overall pattern of relationships revealed by the three methods is the same but there are differences in detail.

2. The unweighted method which measures the similarity between groups by the average similarity between their members (UPGMA) has the highest cophenetic correlation with the original similarity values. It therefore reproduces most accurately the relationships between the forms.

3. The unweighted method which measures the similarity between groups by the distance between their centroids (UPGMC)

has the second highest cophenetic correlation with the original similarity values. It has the advantage that the relationships between groups can be interpreted in geometric terms. It differs from the other methods in that the similarity between groups sometimes increases as new members are added to the groups. This results in "reversals" in the dendrogram. The clusters of forms produced are "tighter" than those produced by the other methods since the distance between the centroids of two groups is always less than the average similarity between their members.

4. The weighted method (WPGMA) has the lowest cophenetic correlation with the original similarity values. A characteristic of this method is that the similarities between forms on the peripheries of clusters are given greater weight when calculating the similarity between the clusters than the similarities between forms near the nuclei of the clusters. When a cluster is equidistant from two others the linkage produced by the weighted method may be the reverse of that produced by the method which uses unweighted averages (UPGMA).

3.4.2 Principal components analysis

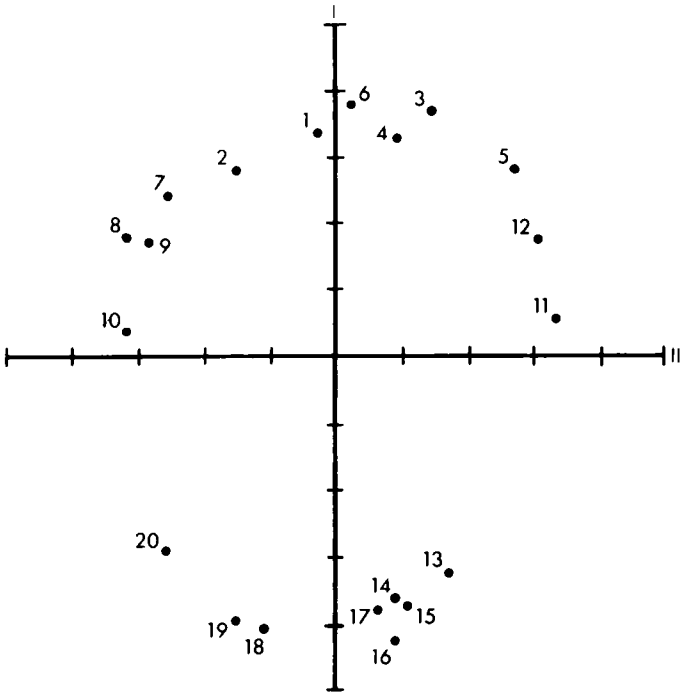
The second solution to the problem of analysing tables of similarity values which is considered here is the method of

principal components analysis. This method was discussed in Section 2.5.2 and was shown to be a means of projecting the forms from the multi-dimensional space in which they lie into a space of reduced dimensions. A projection is obtained which minimises the distortion of the pattern of relationships. In this section, the method is used to analyse tables of correlations and mean square distances between forms. The results are compared with each other and with those obtained by cluster analysis.

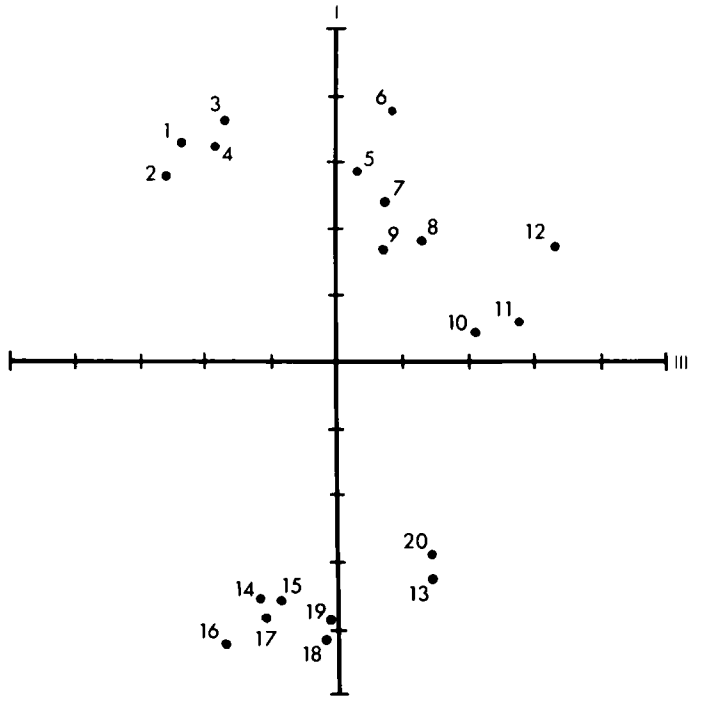
Principal components analysis was applied to a table of correlations based on standardised character values. Latent roots and vectors were extracted from the table and the latent vectors were normalised so that the sum of squares of the elements of each vector was equal to the corresponding latent root. The first four roots and vectors are given in Table 3.6. In Fig. 3.4, the first three latent vectors are used as coordinate axes and the positions of points used to represent the forms are shown with respect to the first and second vector in Fig 3.4 (a) and with respect to the first and third vector in Fig. 3.4 (b). The first three vectors were used in the construction of a model. Two views of this are shown in Fig. 3.5. The vertical axis corresponds to the first latent vector; the model is viewed along the axis corresponding to the third latent vector in Fig. 3.5 (a) and along the axis corresponding

Figure 3.4

Diagram to show the results of a principal components analysis of correlations between hominoid skulls based on standardised character values. (a) Forms plotted with respect to the 1st and 2nd latent vectors. (b) Forms plotted with respect to the 1st and 3rd latent vectors. Reference numbers as in Table 3.1. Each division equals 0.2 units.


I
II
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

a


I
III
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

b

Figure 3.5 (a)

Model to show the results of the principal components analysis of hominoid correlations. The vertical axis corresponds to the 1st latent vector and the horizontal axes to the 2nd and 3rd latent vectors. The model is viewed at right-angles to the 2nd latent vector. Reference numbers on base as in Table 3.1.

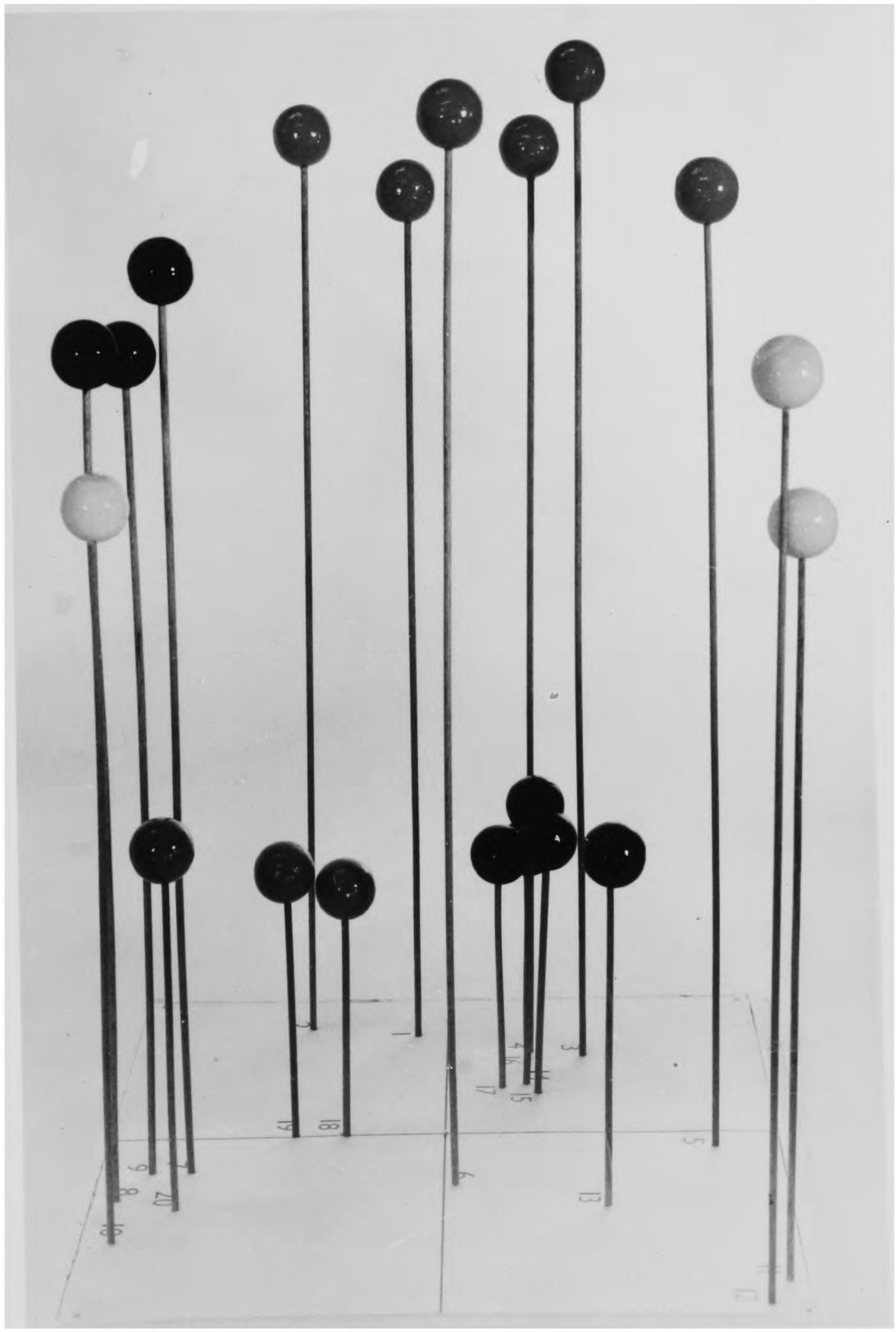
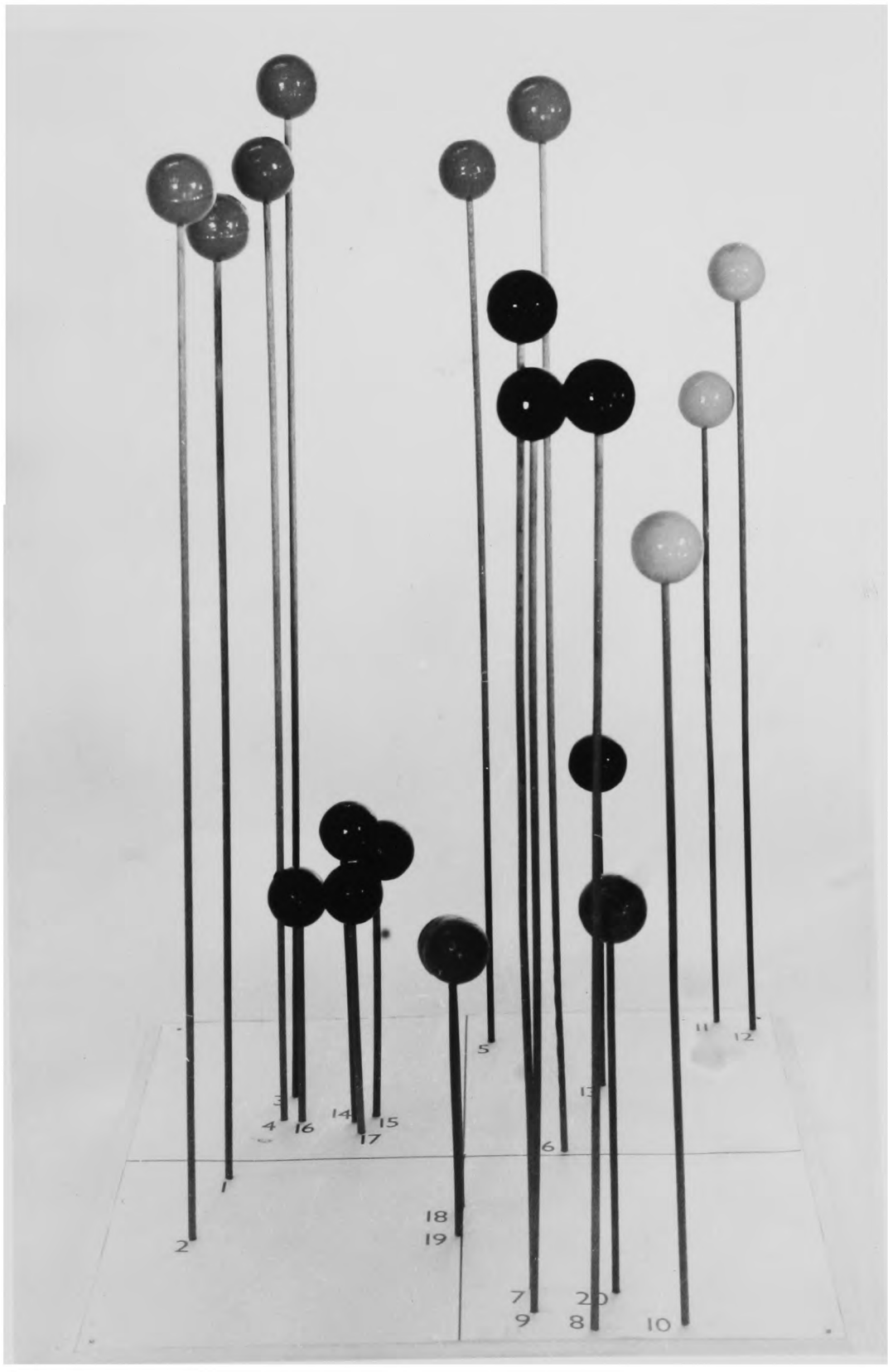

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

Figure 3.5 (b)

Model as in Fig. 3.5 (a) viewed at right-angles to the 3rd latent vector. Reference numbers on base as in Table 3.1.


1
2
3
4
16
14
15
17
5
18
19
6
13
11
12
7
9
20
8
10

to the second vector in Fig. 3.5 (b).

An examination of these figures shows that the forms fall into two quite distinct clusters. The apes and Australopithecines (forms 1 - 12) lie in the upper half of the space and are quite separate from the fossil and modern hominids (forms 13 - 20) which lie in the lower half. Within the ape-Australopithecine cluster there is a division into three sub-clusters (see Fig. 3.5 a). These are a cluster of juvenile forms, a cluster of adult apes and a cluster of adult Australopithecines. Within the hominid cluster there is a division into fossil and modern forms.

How well do these three latent vectors reproduce the original table of correlations? One answer to this question is provided by the latent roots. A latent root is a measure of the amount of variation among the forms accounted for by its corresponding latent vector, since it is the sum of squares of the projections of the forms onto that vector. The success of any group of vectors in accounting for the variation among forms can be measured by the proportion of the total variation (equal to the sum of the main diagonal elements of the similarity table) accounted for by their latent roots. Table 3.6 shows that approximately two-thirds (66.77%) of the total variation is accounted for by the first three latent vectors.

A second method of measuring the distortion produced by

the reduction of dimensions is the method of cophenetic correlations already used to compare the cluster analyses in Section 3.4.1. Cophenetic values are obtained by calculating the distances between all pairs of forms. The distance d_{jk} between forms j and k is given by:

$$d^2_{jk} = (c_{j1} - c_{k1})^2 + (c_{j2} - c_{k2})^2 + (c_{j3} - c_{k3})^2$$

where c_{j1} is the element of the first latent vector corresponding to form j (the coordinate of form j with respect to the first axis of the model); c_{j2} is the element in the second vector and so on. In Section 2.5.2, it was shown that the distances between points (using all latent vectors as coordinate axes) and the correlations between forms are related by the formulae:

$$d^2_{jk} = 2(1 - r_{jk}) \quad .$$

or:

$$r_{jk} = 1 - \tfrac{1}{2} d^2_{jk} \quad .$$

If the distances based on three vectors are transformed into "correlations" by the second formula given above, the new values can be compared with the original correlations and the goodness of fit measured by the method of cophenetic correlations. When this is done, the cophenetic correlation between the results of the principal components analysis (using the first three vectors) and the original correlations

is found to be 0.969. The first three vectors therefore give a very good reproduction of the original correlations. A comparison between this value and the cophenetic correlations of the three methods of cluster analysis with the original correlations (p. 67) shows that the first three latent vectors reproduce the original correlations more faithfully than any of the dendrograms.

The pattern of relationships revealed by the first three vectors is very similar to that revealed by the methods of cluster analysis although it is presented in a less emphatic way. The concordance between the results of the principal components analysis and the three dendrograms can also be measured by cophenetic correlations. The values obtained are:

	WPGMA	UPGMA	UPGMC
PCA	0.817	0.859	0.852

The dendrogram produced by the unweighted method using averages thus shows the best fit with the results of the principal components analysis.

Although cluster analysis produces a diagram in which the groupings are shown clearly and forcefully it suffers from the following disadvantage: the dendrogram shows the relationships between clusters but is only a rough guide to the relationships

between the members of one cluster and those of another. For example, Fig. 3.1 (a) on p.59 shows the link between the cluster of juvenile apes (7, 8, 9) and that of the adult apes and between the juvenile Homo sapiens (20) and the other hominids but gives no clue to the degree of similarity between the juvenile apes and the juvenile H.sapiens. Fig. 3.4, however, not only shows the links between the juveniles and their adults but also shows that the juvenile H. sapiens lies in the direction of the juvenile apes. The diagrams produced by principal components analysis thus show the main clusters although not as sharply as the cluster diagrams and have the advantage of giving more information about the inter-relationships of individual forms than do the cluster diagrams.

In Section 2.5.2 it was shown that principal components analysis can also be applied to tables of distance coefficients providing the distances are first transformed. The method is applied here to a table of transformed mean square distances based on standardised character values. The transformation used is:

$$S_{ij} = 1 - 0.1\, d^2_{ij}$$

where d^2_{ij} is the mean square distance between forms. Since the mean square distance between a form and itself is zero, the elements of the main diagonal of the table of S-values are unities.

The first four latent vectors and their corresponding latent roots are given in Table 3.7. The most marked difference between this table and Table 3.6 is that the elements of the first latent vector of the distances table are nearly constant while those of the first vector of the correlation table show a wide range of positive and negative values. Gower (1965) suggests that a latent vector with more or less constant values may be regarded as representing the mean value of all the elements in the table of similarity values. The mean value of the distances between forms is a measure of the homogeneity of the forms under consideration and although the mean may be useful in comparisons between numerical studies, it may be ignored within a single study. For, as Gower points out, if a constant is added to all the elements in the distance table, the distances between the points given by the principal components analysis remain unchanged. Gower suggests a transformation of the distance values which removes the effect of the mean, but the simpler approach adopted here is to ignore the first latent vector and to examine the pattern of relationships shown by the second, third and fourth vectors.

The table of correlations, on the other hand, has a mean which is very close to zero ($\bar{X} = -0.061$) and therefore a latent vector with almost constant elements is not produced. The low mean value is the result of standardising the

character values on which the correlations are based. It was pointed out in Section 2.3 (p. 16) that standardisation is the combination of a translation and a change of scale. The change of scale affects both distances and correlations but the translation of the origin of the character space to the centroid of the cluster of forms affects only the correlations. Since, in this particular study, the forms are more or less evenly distributed around their centroid (see Fig. 3.5 a) more or less equal numbers of positive and negative correlations are obtained. Their mean is therefore close to zero.

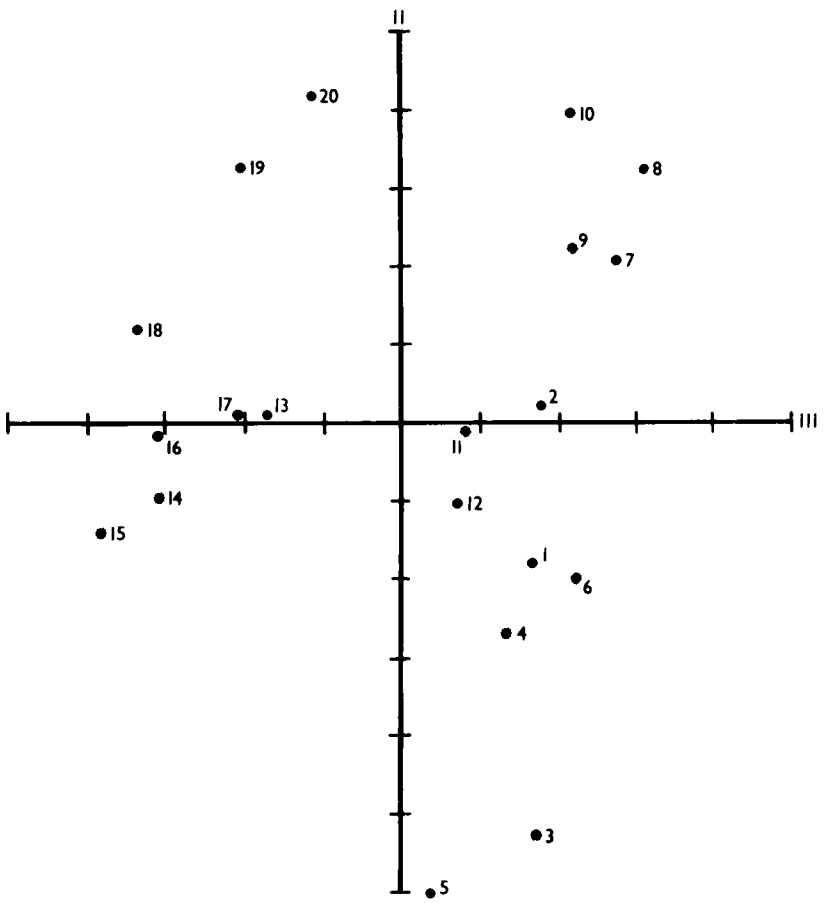
The results of the principal components analysis of the table of mean square distances are shown in Fig. 3.6 and Fig. 3.7. In Fig. 3.6 (a), the forms are plotted with respect to the second and third latent vectors; in Fig. 3.6 (b), with respect to the second and fourth latent vectors. In Fig. 3.7, Fig. 3.6 (a) is put beside the dendrogram produced by the unweighted average cluster analysis. This is done in order to aid comparison of the results of the two methods.

An examination of Fig. 3.6 shows that the forms fall into five main clusters. These are (i) the adult apes (excluding the male orang and gorilla) and the adult Australopithecines (forms 1, 2, 4, 6, 11, 12), (ii) the juvenile apes and the juvenile Australopithecine (forms 7 - 10), (iii) the fossil hominids (forms 13 - 17), (iv) the modern hominids (forms 18 - 20,

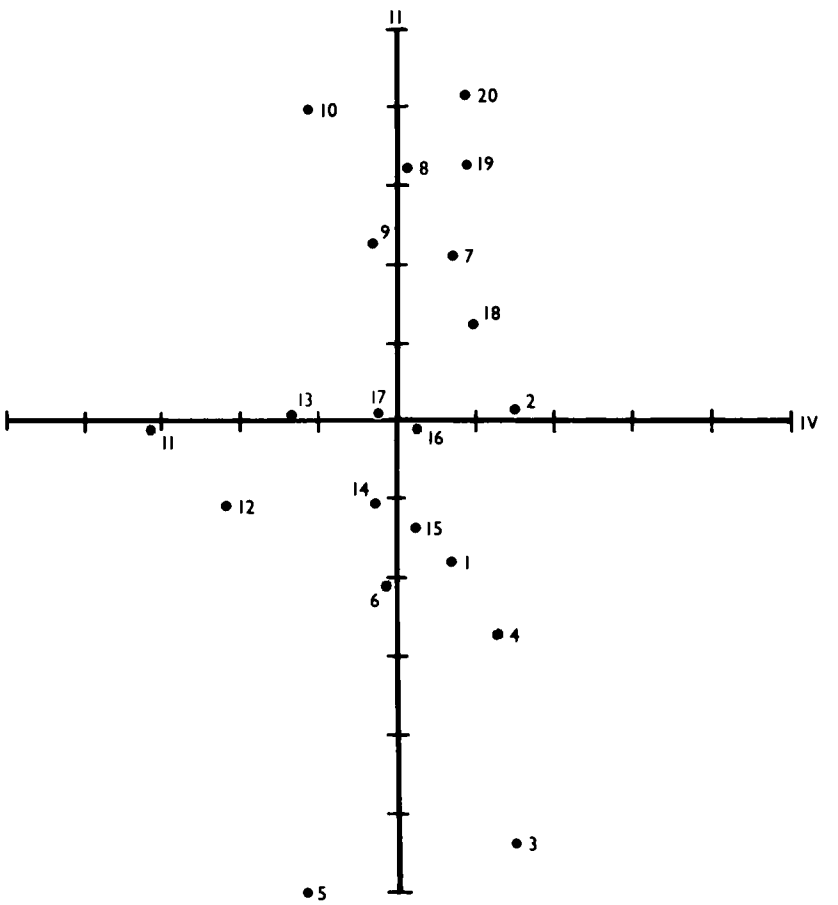
Figure 3.6

Diagram to show the results of a principal components analysis of mean square distances between hominoid skulls based on standardised character values.
(a) Forms plotted with respect to the 2nd and 3rd latent vectors. (b) Forms plotted with respect to 2nd and 4th latent vectors.

Reference numbers as in Table 3.1. Each division equals 0.1 units.


II
III
20
10
19
8
9
7
18
17
13
2
16
11
14
12
15
1
6
4
3
5

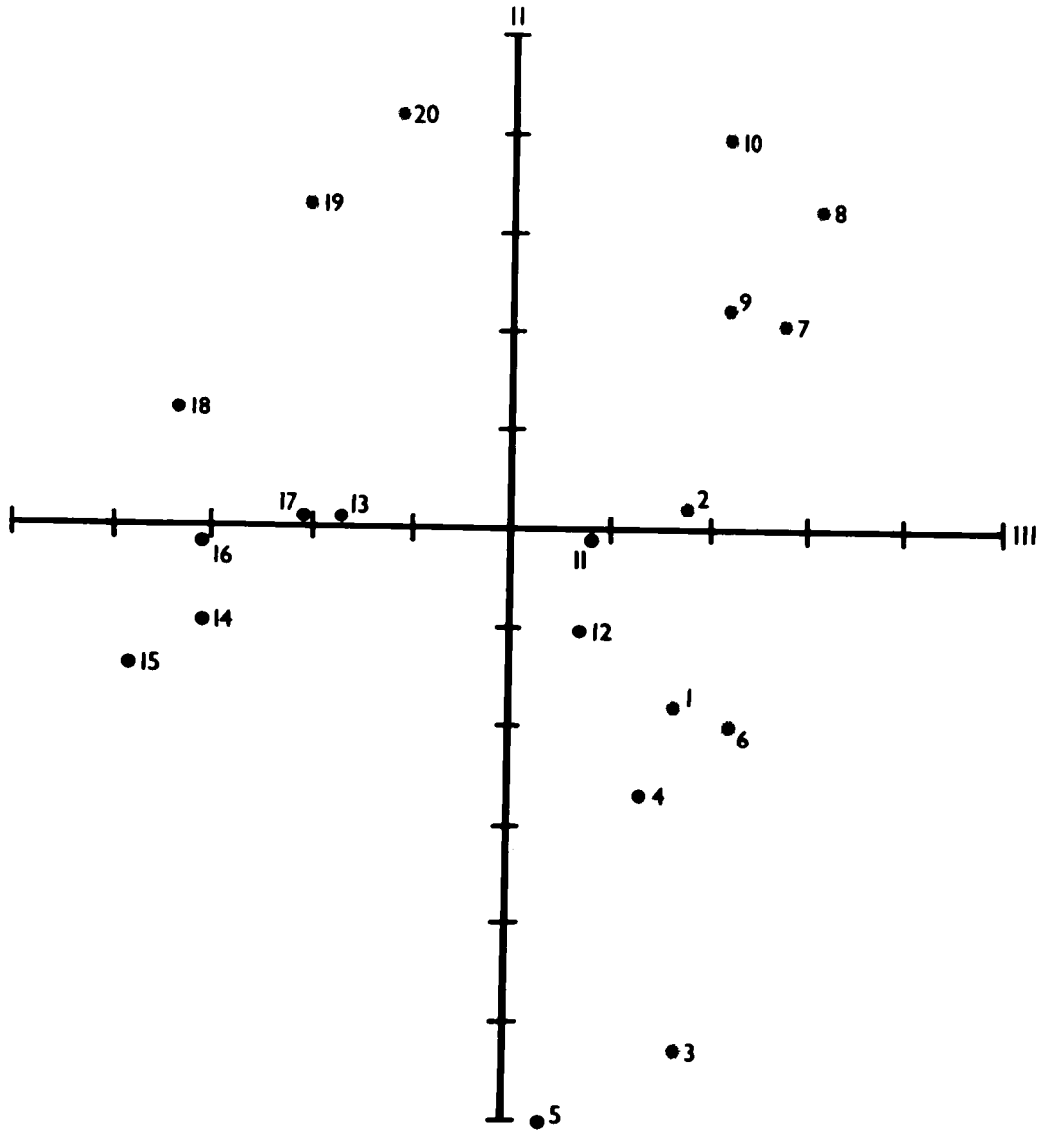
a


II
IV
10
20
8
19
9
7
18
13
17
2
11
16
14
12
15
1
6
4
3
5

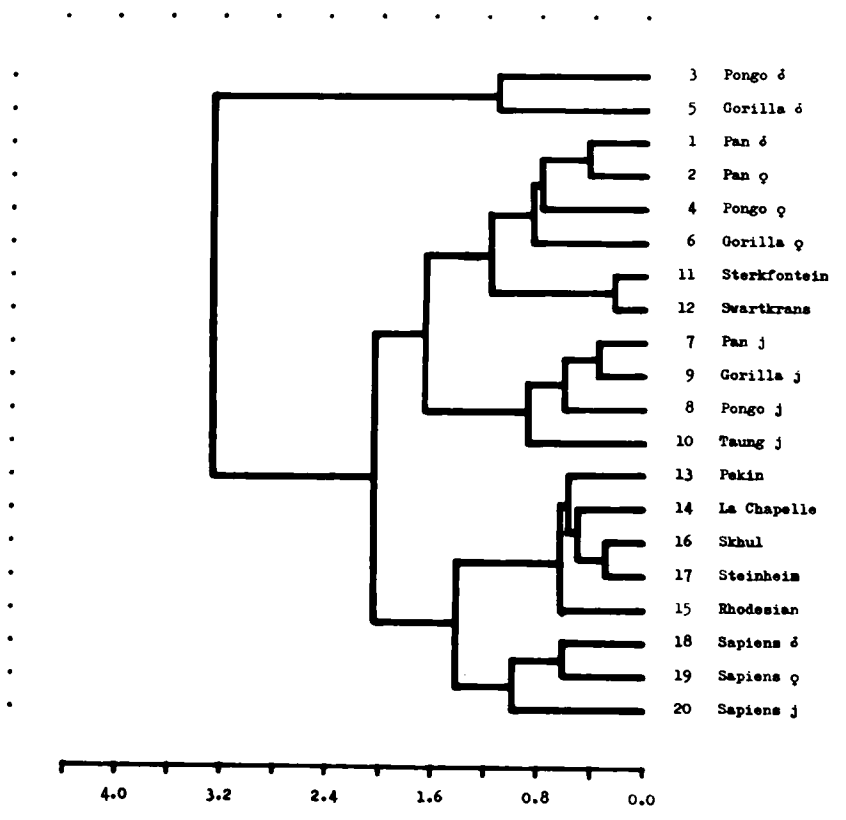
b

Figure 3.7

Comparison between principal components analysis and cluster analysis of mean square distances. (a) Forms plotted with respect to the second and third latent vectors. (b) Dendrogram produced by unweighted average pair-group cluster analysis.


II
III
20
10
19
8
9
7
18
17
13
2
16
11
14
12
15
1
6
4
3
5

a


3 Pongo ♂
5 Gorilla ♂
1 Pan ♂
2 Pan ♀
4 Pongo ♀
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
16 Skhul
17 Steinheim
15 Rhodesian
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
4.0
3.2
2.4
1.6
0.8
0.0

b

and (v) the male orang and gorilla (forms 3 and 5). These five clusters can be recognised in the dendrogram produced by the unweighted average method of cluster analysis (Fig. 3.7 b). The agreement between the results of the two methods, judged by a visual comparison, is quite good but there are a number of differences in detail. For example, in the principal components diagram the male and female chimpanzees (1, 2) are widely separated whereas in the dendrogram they show a very close linkage. A similar separation in the principal components diagrams and close linkage in the dendrogram is shown by the male and female Homo sapiens (18, 19).

Two methods of measuring the agreement between the results of a principal components analysis and the table of similarity values on which the analysis is based were discussed on p.74 The first method considers the amount of variation accounted for by the subset of latent vectors used to represent the forms. In the analysis of mean square distances, the variation among forms accounted for by the first latent vector is 81.7% of the total variation. This vector is not used in the representation of the forms since it is thought to represent simply the magnitude of the distances between forms and not their relative differences (which determine the pattern of relationships). Of the remaining variation, 77.0% (see Table 3.7) is accounted for by the second, third and fourth vectors and it

is reasonable to suppose that the distortion of relationships produced by using only these three vectors is small.

The second method is that of cophenetic correlations. The distances between the points in the principal components diagram were calculated using the elements of the second, third and fourth vectors as coordinates. The agreement between these distances and the original mean square distances was measured by the correlation coefficient and this was found to be 0.992. This high correlation indicates that the representation of relationships by these three vectors is very good.

The main conclusions which can be drawn from this study of principal components analysis are:

1. Principal components analysis is an effective method of analysing the multi-dimensional relationships between forms contained in a table of similarity values. It can be applied with equal success to tables of correlations and distances (provided these are first transformed).

2. The method was applied here to a table of correlations and to a table of mean square distances, both based on standardised character values. The first three latent vectors of the table of correlations gave a good representation of the original correlations (cophenetic correlation = 0.969). The first latent vector of the distance table was found to have almost constant values and was thought to represent only the

the magnitude of the distances and not their relative differences. A good representation of the original mean square distances was obtained by using the second, third and fourth latent vectors (cophenetic correlation = 0.992). The advantage of representing relationships with only three vectors is that the relationships can be shown clearly by means of a solid model or pair of two-dimensional projections of this model.

3. The agreement between the results of principal components analysis and cluster analysis is close. Principal components analysis gives a slightly better reproduction of the original similarity values and gives more information about the relationships of individual forms than cluster analysis.

3.5 Measurements of similarity

The problem of measuring similarity between forms was considered in Section 2.4 and five coefficients were discussed. These were the cosine of the angle between forms, the correlation coefficient, the mean square distance, the mean character difference and Penrose's shape coefficient. In this section, the performance of these five coefficients is considered. In order to compare the five coefficients, a means of analysing the information they provide about relationships is needed. The unweighted pair-group method of cluster analysis which uses averages to measure the similarity between groups is used

here because it gives a better reproduction of a table of similarity values than the other methods of cluster analysis considered here and because it expresses relationships in a more easily understood form than does principal components analysis. It has the additional advantage that the calculations it involves are simpler than those involved in principal components analysis.

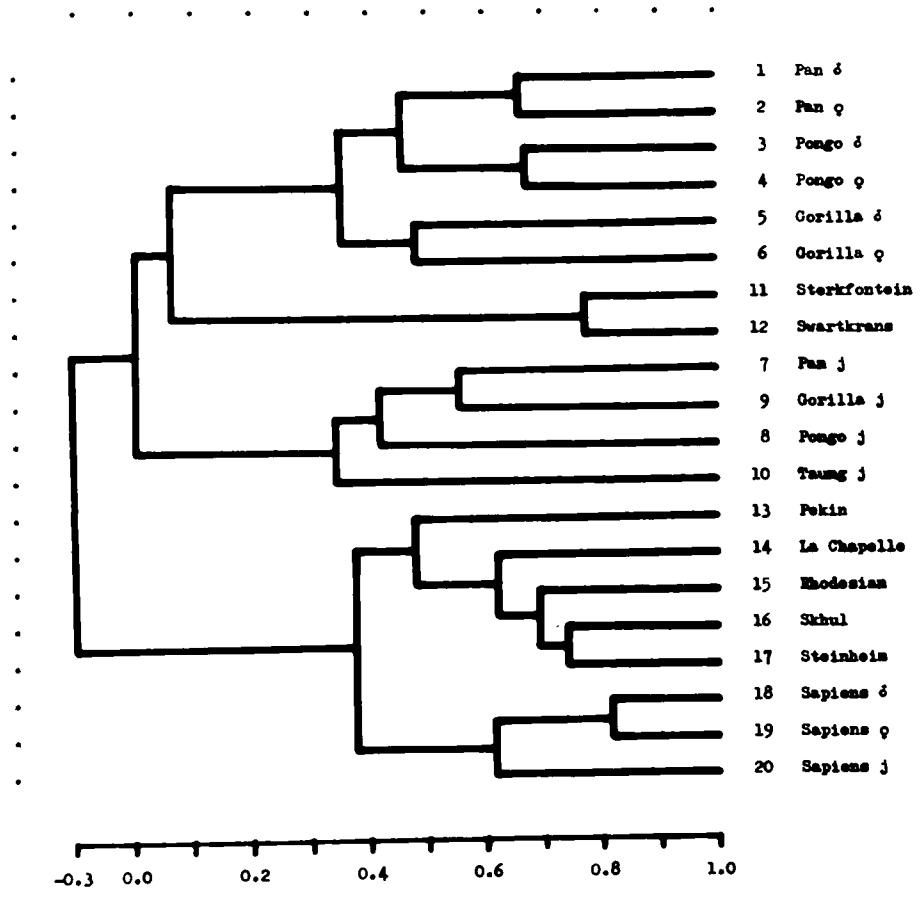
Measurements of similarity, using the five coefficients, were made between twenty hominoid skulls. The skulls and the characters used to describe them were discussed in Sections 3.2 and 3.3 and are listed in Tables 3.1 and 3.2. The same character values were used in the calculation of each of the five sets of coefficients and were obtained by standardising the raw data values (given in Table 3.4). The similarities between each pair of skulls, measured by the five coefficients, are given in Table 3.5. The results of analysing the five sets of similarity values are presented in Fig. 3.8 and Fig. 3.9.

Fig. 3.8 shows the patterns of relationships produced by the two angular coefficients discussed in Section 2.4.1. Fig. 3.8 (a) is a dendrogram based on correlations between the skulls and Fig. 3.8 (b) is a dendrogram based on cosines of angles between the skulls. The main clusters into which the forms fall and the linkages between clusters are the same in both dendrograms. The patterns of relationship within the main

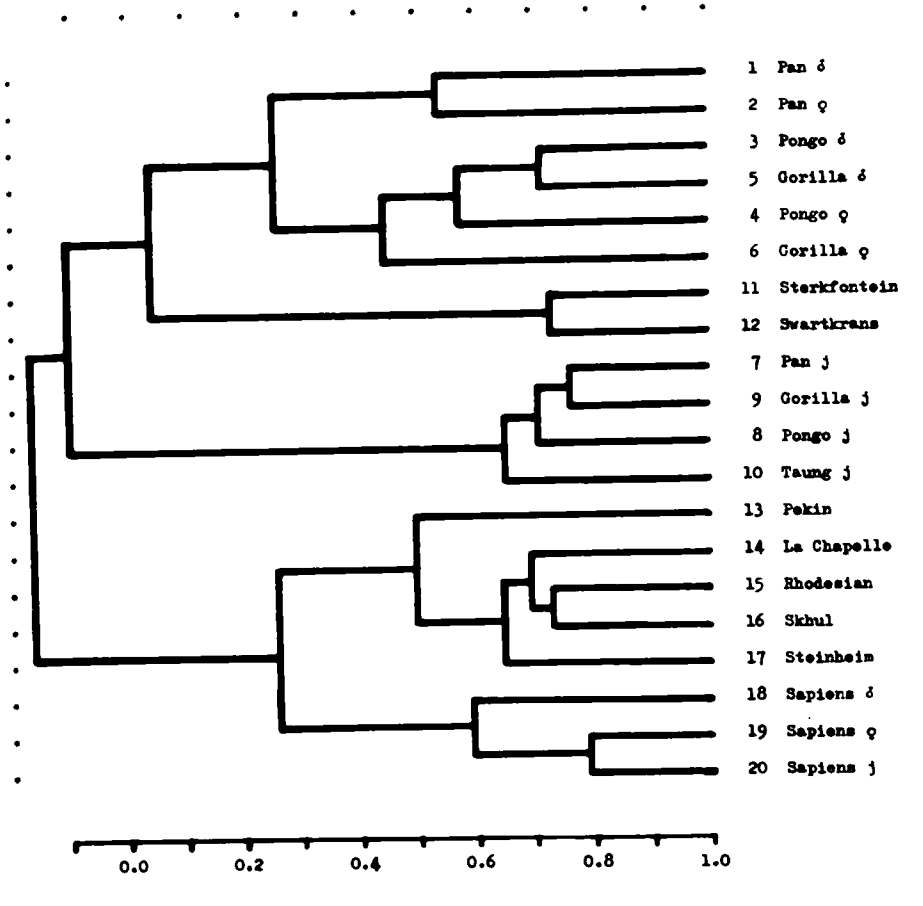
Figure 3.8

Patterns of relationship shown by correlation coefficients (a) and cosines of angles (b).

Dendrograms produced by unweighted average pair-group cluster analysis of similarities based on standardised character values.


1 Pan ♂
2 Pan ♀
3 Pongo ♂
4 Pongo ♀
5 Gorilla ♂
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
-0.3 0.0 0.2 0.4 0.6 0.8 1.0

a


1 Pan ♂
2 Pan ♀
3 Pongo ♂
5 Gorilla ♂
4 Pongo ♀
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
0.0 0.2 0.4 0.6 0.8 1.0

b

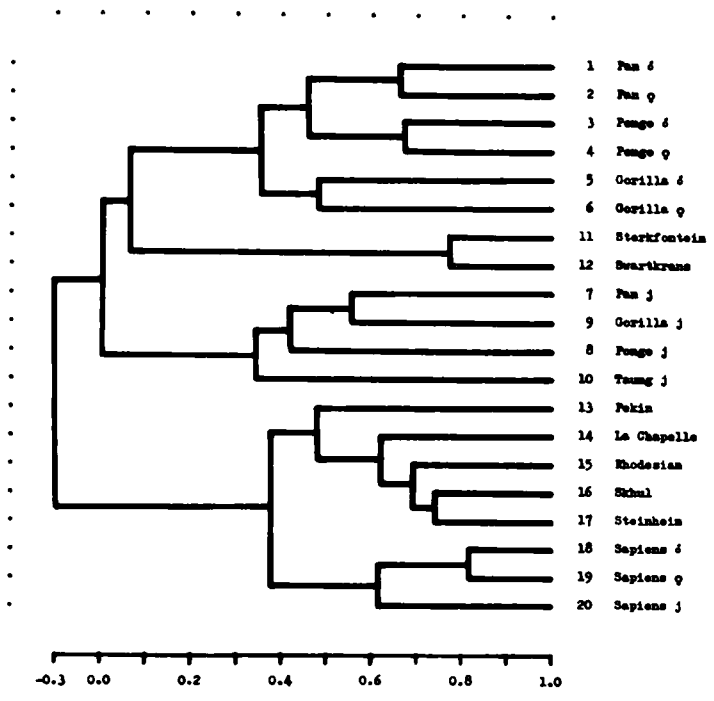
clusters, however, are not the same. When similarity is measured by the correlation coefficient, the male apes and the male Homo sapiens are most similar to their corresponding females. When similarity is measured by the cosine of the angle between two forms, however, the male orang and the male gorilla are more similar to each other than to their corresponding females and the female Homo sapiens is more similar to the juvenile than to the male Homo sapiens. Within the fossil hominid group, the pattern of relationships also varies according to the coefficient of similarity used.

Fig. 3.9 compares the pattern of relationships shown by the correlation coefficient with that shown by the three distance coefficients discussed in Section 2.4.2. In Fig. 3.9, dendrogram (a) is based on the correlation coefficient, (b) on the mean square distance, (c) on Penrose's shape coefficient and (d) on the mean character difference. A comparison between the dendrograms shows that irrespective of the coefficient used to measure similarity the same overall pattern of relationships emerges. The pongids are clearly separated from the hominids ; within the pongids there is a division into adult and juvenile forms and within the hominids, a division into fossil and modern forms. The Australopithecines always show a greater similarity with the pongids than with the hominids. When similarity is measured by means of distance

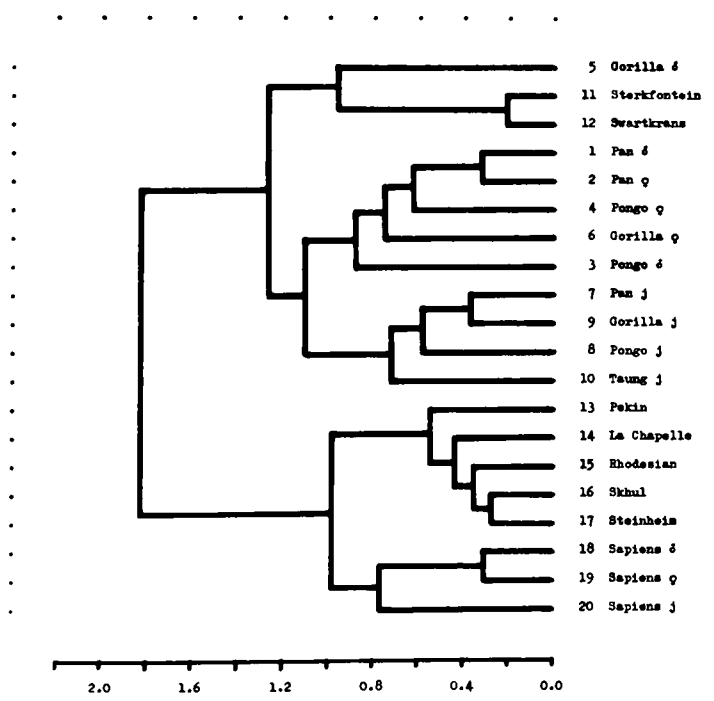
Figure 3.9

Patterns of relationship shown by correlation coefficients (a), mean square distances (b), Penrose's shape coefficients (c), and mean character differences (d).

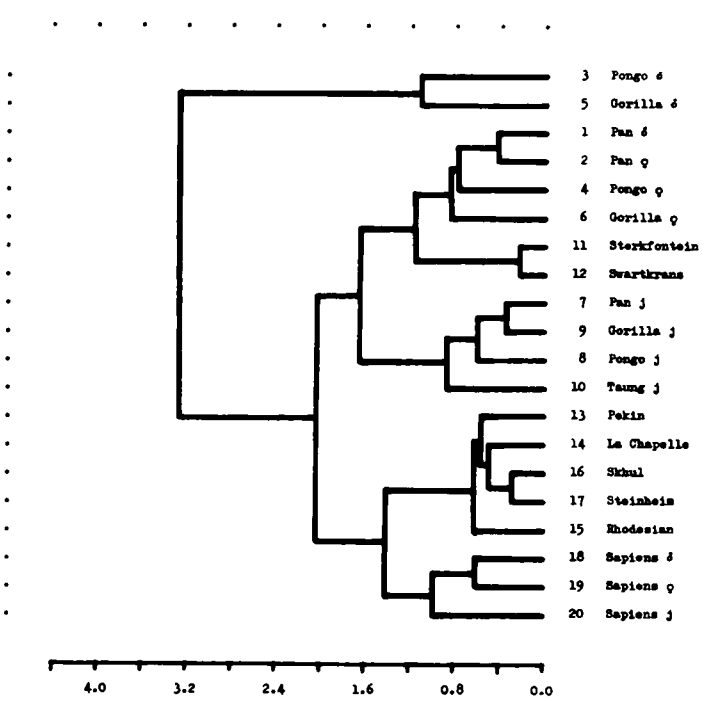
Dendrograms produced by unweighted average pair-group cluster analysis of similarities based on standardised character values.


1 Pan ♂
2 Pan ♀
3 Pongo ♂
4 Pongo ♀
5 Gorilla ♂
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
-0.3 0.0 0.2 0.4 0.6 0.8 1.0

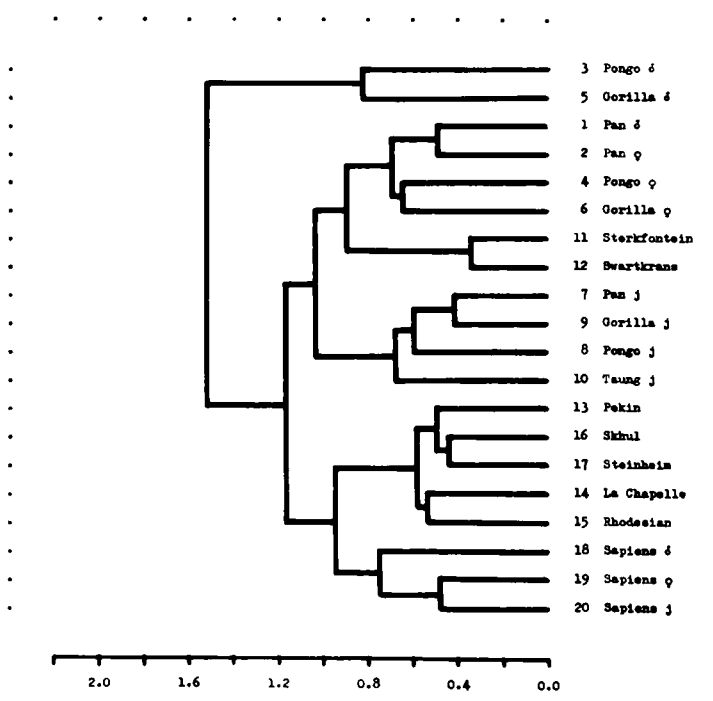
a


5 Gorilla ♂
11 Sterkfontein
12 Swartkrans
1 Pan ♂
2 Pan ♀
4 Pongo ♀
6 Gorilla ♀
3 Pongo ♂
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
15 Rhodesian
16 Skhul
17 Steinheim
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
2.0 1.6 1.2 0.8 0.4 0.0

c


3 Pongo ♂
5 Gorilla ♂
1 Pan ♂
2 Pan ♀
4 Pongo ♀
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
14 La Chapelle
16 Skhul
17 Steinheim
15 Rhodesian
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
4.0 3.2 2.4 1.6 0.8 0.0

b


3 Pongo ♂
5 Gorilla ♂
1 Pan ♂
2 Pan ♀
4 Pongo ♀
6 Gorilla ♀
11 Sterkfontein
12 Swartkrans
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
13 Pekin
16 Skhul
17 Steinheim
14 La Chapelle
15 Rhodesian
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
2.0 1.6 1.2 0.8 0.4 0.0

d

coefficients, however, the male orang and gorilla show less similarity with their corresponding females than when similarity is measured by the correlation coefficient and in the dendrograms based on mean square distances and mean character differences, the male orang and gorilla form a cluster which is quite separate from the other main clusters. Within the main clusters, there is some variation in the patterns of relationship according to the coefficient used to measure similarity.

What conclusions can be drawn from this comparison of the five methods of measuring similarity? It is important to remember, when considering the differences between dendrograms, that the pattern of relationships shown by a dendrogram is only an approximate representation of the table of similarities between forms on which it is based and that small variations in the similarities between forms are sufficient to alter the linkages. In assessing the relative merits of the five methods, therefore, too much emphasis cannot be placed on minor differences between the dendrograms.

The position of the male orang and gorilla, however, shows a very striking variation among the five dendrograms and an examination of the nature of the differences between the male orang and gorilla and their corresponding females

throws light on the kind of "resemblance" measured by the five methods. Orangs and gorillas show a high degree of sexual dimorphism. This takes the form, in the males, of an overall increase in size and an exaggerated development of certain parts of the skull (for instance, the development of sagittal and occipital crests) as a result of an increase in the size of the jaw. An examination of the differences in the (standardised) character values of the male and female gorilla skulls confirms the conclusion that the differences between the males and females are mainly size differences. In Table 3.9 are listed the twenty characters which show the largest absolute differences in value. The character values are listed in descending order of absolute magnitude. These values account for 42.7% of the total difference in character values between the two skulls. Of the twenty characters, only two (14, 18) have a smaller value in the male. The differences in character values are not constant and, furthermore, the characters are not evenly distributed over the skull but are mainly features of the jaw and of the temporal and occipital regions. The differences in size between the skulls of the male and female gorilla are therefore proportional as well as additive differences.

If the five coefficients are ordered according to the

degree of isolation shown by the male orang and gorilla, the order is: correlation coefficient (least isolation), cosine of angle, shape coefficient, mean character difference, mean square distance. Since the difference between the male and female in the orang and gorilla is mainly a difference in size, it is reasonable to conclude that the differences between the dendrograms reflect mainly differences in sensitivity to size on the part of the five coefficients. In Section 2.4, it was suggested that the angular coefficients are less sensitive to size than the distance coefficients and although the normalising properties of the coefficients are to some extent affected by standardising the character values (see next section) the performance of the coefficients does agree with that suggested on theoretical grounds.

The main conclusionswhich can be drawn from this comparative study of five methods of measuring similarity are as follows: the agreement between the patterns of relationship shown by the five coefficients is close. The differences which do appear are mainly the result of the relative emphasis placed by the different coefficients on the size component of overall resemblance. Of the five coefficients, the correlation coefficient reacts to the components of size and shape in a way most

similar to that which the taxonomist usually adopts since it links together the males and females of each of the four modern groups.

3.6 Transformation of character values

In Section 2.3, the problem of character transformation was considered and a distinction was made between the use of a transformation to remove the effect of differences in the units in which characters are expressed and the use of a transformation to increase the sensitivity of coefficients to particular components of resemblance. One particular transformation, standardisation, has been employed in all the comparisons between the methods made in earlier sections of this chapter. This transformation was necessary because some of the characters were measured in different units. However, the majority of characters were measured in the same units and it is of interest to inquire into the effects of transformation on these characters. The particular transformation used in this study, standardisation, is the combination of a change of scale and a translation (p.18). The change of scale affects both distance and angular coefficients whereas the translation affects only angular coefficients. It is convenient, therefore, to discuss the two components separately.

The effect of the change of scale is to equalise the scatter of forms in the character space in directions parallel to the character axes. Since the larger the scatter of forms is along a direction parallel to a character axis, the larger on average is the contribution made by that character to a coefficient of resemblance, the effect of equalising the scatter of forms is to equalise the contributions of different characters. Since the coefficients are intended to measure overall resemblance, it seems appropriate that their contributions should be equal. If the change of scale is not carried out then those characters which show most variation will tend to dominate the measures of resemblance and the information these provide will be reduced. The effect of the change of scale therefore is to increase the sensitivity of the coefficients to the subtler differences among the forms.

The translation of the origin of the character space to the centroid of the cluster of forms has no effect upon the distances between the forms but greatly changes their angular separation. The lines connecting the forms to the origin of the character space are a bundle and the angles between the lines are small. The lines connecting the forms to the centroid of the cluster of forms, however, radiate in all directions with many large angles between them.

Sneath (manuscript in preparation) points out that the distance of a form from the centroid of the cluster of forms is a measure of its typicality, that is the degree to which it is representative of the group of forms being studied. He suggests that the angular separation of two forms viewed from the centroid is a measure of their distinctiveness, that is their similarity after removing the element of typicality. The cosine of the angle between two forms is therefore also a measure of distinctiveness when it is based on standardised character values.

Rohlf and Sokal (1965) have suggested that if the characters used to describe the forms are standardised then the mean of the character values of each form will be close to zero. If this were so, then the correlation between two forms would approximate to the cosine of the angle between them and would, therefore, also be a measure of their distinctiveness. However, the mean of the character values of a form will be close to zero only if it differs from the "average" (i.e. the centroid of the cluster of forms) mainly in shape. For, only if it differs in shape will some of its character values (after standardisation) be negative and others positive and tend to have a small mean value. If it differs from the average mainly in size, on the other hand, its character values will be mainly positive or mainly negative

and their mean will tend to have a large absolute value. If the distinctiveness of two forms is due mainly to a difference in size, their angular separation will appear less when measured by the correlation coefficient than when measured by the cosine. If, on the other hand, their distinctiveness is due mainly to a difference in shape, their angular separation will appear the same whether measured by the correlation coefficient or the cosine. The correlation coefficient will, therefore, be less sensitive than the cosine to differences in size when the character values of the forms are standardised.

This discussion has shown that the effects on measures of resemblance of even a relatively simple transformation such as standardisation are quite complex. It is not easy, simply by examining these effects from a theoretical point of view, to decide whether they increase the taxonomic usefulness of the measures of resemblance. Further evidence with which to judge the merits of standardisation can be obtained, however, by comparing the pattern of relationships produced by a measure of resemblance based on standardised characters with that produced by the same measure based on unstandardised characters.

Such a comparison has been made for the correlation coefficient. Correlations between the twenty hominoid skulls were calculated on the basis of standardised and

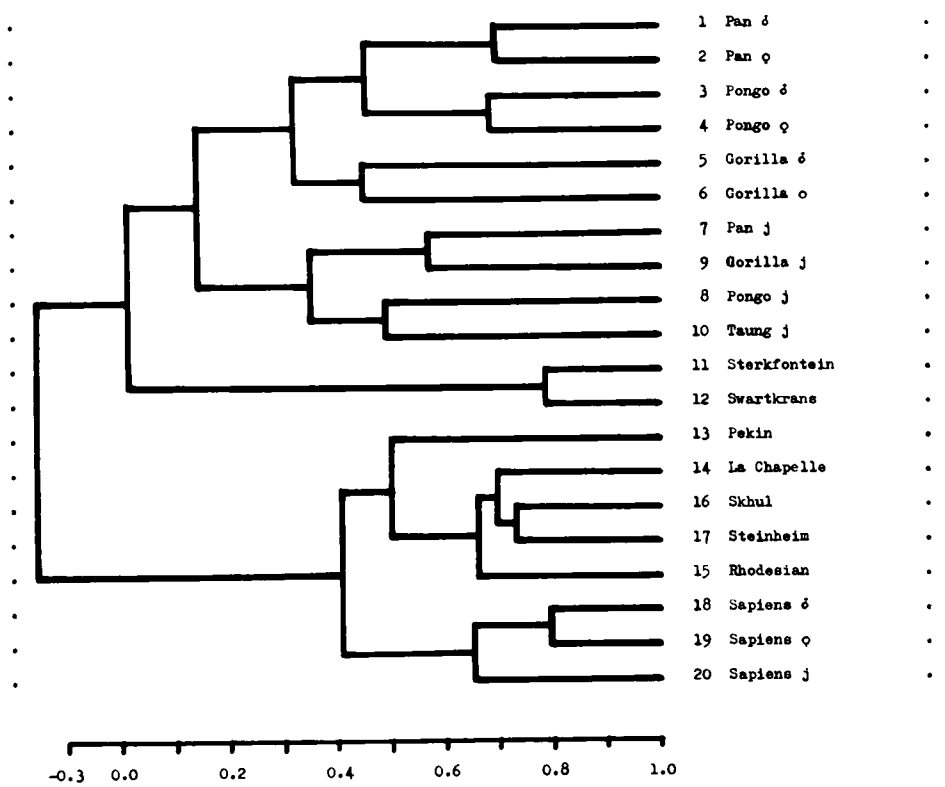
unstandardised character values. In order to remove the effect of differences in units, only those characters measured in the same unit were included. 14 of the 99 characters used to describe the skulls were therefore ignored. These were characters 8, 15, 16, 17, 18, 36, 44, 57, 71, 76, 77, 79, 80, 99 (see Table 3.3). The correlations were analysed by the unweighted pair-group method of cluster analysis and the dendrograms produced by this analysis are shown in Fig. 3.10. Fig. 3.10 (a) is based on standardised character values and Fig. 3.10 (b) on unstandardised character values.

Several points emerge from a comparison of the two dendrograms. The dendrograms show clearly the marked effect standardisation has upon the correlation coefficient. When the character values are unstandardised, the correlations among the skulls are very high and this indicates that they form a tight cluster some distance from the origin of the character space. The average correlation among the skulls gives a measure of the tightness of this cluster and would be of value in comparing the average degree of resemblance shown by these forms with that shown by other groups. When the character values are standardised, however, the average correlation among the skulls is low and is the result of viewing the relationships of the skulls from the centroid of

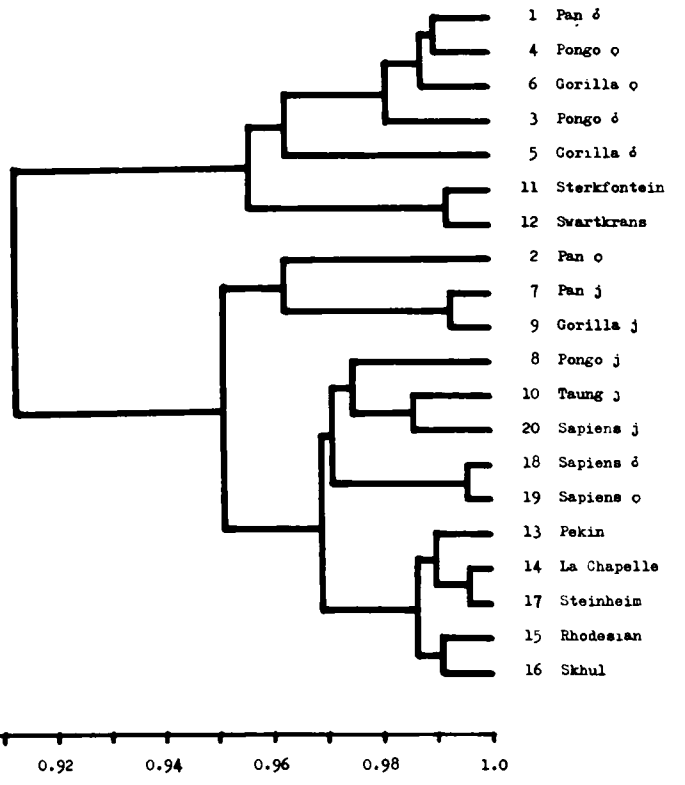
Figure 3.10

Patterns of relationship shown by correlations based on standardised character values (a) and unstandardised character values (b).

Dendrograms produced by unweighted average pair-group cluster analysis.


1 Pan ♂
2 Pan ♀
3 Pongo ♂
4 Pongo ♀
5 Gorilla ♂
6 Gorilla ♀
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
11 Sterkfontein
12 Swartkrans
13 Pekin
14 La Chapelle
16 Skhul
17 Steinheim
15 Rhodesian
18 Sapiens ♂
19 Sapiens ♀
20 Sapiens j
-0.3 0.0 0.2 0.4 0.6 0.8 1.0

a


1 Pan ♂
4 Pongo ♀
6 Gorilla ♀
3 Pongo ♂
5 Gorilla ♂
11 Sterkfontein
12 Swartkrans
2 Pan ♀
7 Pan j
9 Gorilla j
8 Pongo j
10 Taung j
20 Sapiens j
18 Sapiens ♂
19 Sapiens ♀
13 Pekin
14 La Chapelle
17 Steinheim
15 Rhodesian
16 Skhul
0.90 0.92 0.94 0.96 0.98 1.0

b

their cluster in the character space. The pattern of relationships based on standardised characters is more in agreement with that arrived at by intuitive assessments of the similarities between the skulls than is the pattern based on unstandardised characters.

This comparison, although based on only one measure of similarity, the correlation coefficient, does suggest that standardisation of character values should be carried out even when these are all measured in the same unit.

3.7 Summary

The purpose of this chapter has been to make comparisons between a number of quantitative methods of studying taxonomic relationships and to discuss the relative merits of these methods. In order to provide data on which to base these comparisons 99 characters of the skulls of 20 hominoids were expressed in quantitative terms. Three criteria were used in choosing these characters. Firstly, an attempt was made to choose characters from all parts of the skull to ensure that the measures of resemblance were measures of overall resemblance; secondly, non-varying characters were considered to provide redundant information about resemblance and were therefore ignored; thirdly, a functional approach to character definition was considered to provide more information about

the skulls than a purely geometric approach.

The problem of character transformation was discussed and it was shown that even a relatively simple transformation such as standardisation has a profound effect upon the coefficients of similarity. It was suggested that, even when all characters are measured in the same unit, standardisation is useful since the patterns of relationships based on standardised character values are more meaningful than those based on unstandardised values.

Five methods of measuring resemblance quantitatively were considered and the patterns of relationships produced by these were found to be very similar. The most marked variations were found in the patterns of relationships produced by distance coefficients and these variations were attributed to the greater sensitivity to differences in size shown by these coefficients. Of the five coefficients, the correlation coefficient produced the pattern of relationships most similar to that arrived at by intuitive methods.

The effectiveness of a number of methods of analysing tables of similarity values was considered. Three methods of cluster analysis were discussed and the two methods which give equal weight to the members of clusters when measuring the similarity between clusters were found to reproduce the tables of similarity values more faithfully than the

method which gives greater weight to forms which join clusters late in the clustering process. The method of principal components analysis was also investigated. This form of analysis necessitates more computation than does a cluster analysis and its results show the pattern of relationships in a less emphatic and straightforward way than do those of cluster analysis. However, it gives more information about the inter-relationships of individual forms and represents a table of similarity values more accurately than does cluster analysis. It can be applied to both angular and distance coefficients.

TABLE 3.1

LIST OF HOMINOID SKULLS MEASURED

PONGIDAE	Pan ♂	1
	Pan ♀	2
	Pongo ♂	3
	Pongo ♀	4
	Gorilla ♂	5
	Gorilla ♀	6
	Pan j	7
	Pongo j	8
	Gorilla j	9
AUSTRALOPITHECUS	Taung j	10
	Sterkfontein	11
	Swartkrans	12
HOMINIDAE	Pekin (Choukoutien)	13
	La Chapelle aux Saints	14
	Rhodesian (Broken Hill)	15
	Skhul (Mount Carmel)	16
	Steinheim	17
	Homo sapiens ♂	18
	Homo sapiens ♀	19
	Homo sapiens j	20

Each skull was given a reference number and these numbers appear in the right-hand column. j = juvenile.

TABLE 3.2

FUNCTIONAL AREAS OF THE SKULL
AND NUMBER OF CHARACTERS SAMPLED FROM EACH

1.	Torus	5
2.	Orbit	4
3.	Nasal chamber	8
4.	Upper jaw	18
5.	Cheek region	9
6.	Articular region	6
7.	Calvarium	7
8.	Temporal region	5
9.	Occipital region	9
10.	Foramen magnum	4
11.	Mastoid process	1
12.	Tympanic region	1
13.	Basicranial strut	1
14.	Lower jaw	21

TABLE 3.3

LIST OF HOMINOID SKULL CHARACTERS*

TORUS

1 Antero-posterior development in the MSP. From glabella to the point of inflection behind. (tape)

2 Antero-posterior development and vertical thickness above the orbit. From the highest point on the orbital margin to the point of inflection behind. (tape)

3 Lateral development. Width along a line bisecting the angle between a horizontal tangent to the upper orbital margin and a vertical tangent to the lateral orbital margin.(tape)

4 Lateral extension. Distance along the upper border of the torus between points on the lateral borders at the level of glabella. (tape)

5 Lateral extension. Minimum distance between points on the lateral borders of the torus at the level of glabella.

ORBIT

6 Maximum vertical height.

7 Maximum horizontal width.

8 Conformation of bones on medial wall. Length of the suture between ethmoid and lachrymal (+) or between frontal and maxilla (-).

9 Minimum distance between medial borders of the lachrymal grooves.

NASAL CHAMBER

10 Distance in the MSP from the highest point on the nasal bones to the lowest.

*Measurements, unless otherwise specified, are taken with calipers. Horizontal/vertical measurements are parallel with and perpendicular to the Frankfurt Horizontal. MSP = median sagittal plane.

TABLE 3.3 - Continued

11	Horizontal distance between the most lateral points on the nasal bones.
12	Height of the nasal aperture in the MSP. From the lowest point on the nasal bones to the inner curve of the nasal sill (excluding nasal spine, if present).
13	Maximum horizontal breadth of the nasal aperture.
14	Vertical distance from the midpoint of the inner curve of the nasal sill (excluding nasal spine, if present) to the level of maximum breadth.
15	Degree of elevation of nasal bones (ranked 0 - 10).
16	Degree of development of nasal sill (ranked 0 - 5).
17	Degree of development of nasal spine (ranked 0 - 5).
UPPER JAW	
18	Degree of exposure of the facial and palatal components of the premaxilla-maxilla suture (ranked 0 - 10).
19	Degree of alveolar prognathism. Horizontal distance in the MSP from the inner curve of the nasal sill (excluding nasal spine, if present) to the vertical projection of alveolare.
20	Degree of alveolar prognathism. Vertical distance in the MSP from alveolare to the horizontal projection of the midpoint of the inner curve of the nasal sill (excluding nasal spine, if present).
21	Curvature of the incisor row. Distance between the most posterior points on the borders of the lateral incisor sockets.
22	Curvature of the incisor row. Distance in the MSP between a tangent to the posterior borders of the medial incisor sockets and a tangent to the posterior borders of the lateral incisor sockets.
23	Length of the incisor row. From the most medial point on the border of the medial incisor socket to the most lateral point on the border of the lateral incisor socket.

TABLE 3.3- Continued

24	Distance between the most anterior and the most posterior points on the border of the medial incisor socket.
25	Length of the diastema. Minimum distance between the borders of the lateral incisor socket and the canine socket.
26	Maximum length of the canine socket.
27	Maximum width of the canine socket perpendicular to the maximum length.
28	Length of the premolar region. Minimum distance between lines perpendicular to the MSP and tangent to the anterior border of the first premolar socket and the posterior border of the second premolar socket.
29	Length of the molar region. Minimum distance between lines perpendicular to the MSP and tangent to the anterior border of the first molar socket and the posterior border of the most posterior molar visible.
30	Distance between the most medial and the most lateral points on the border of the second molar socket.
31	Total length of the tooth row. From the most posterior point on the alveolar tuberosity to alveolare along the lingual surface of the alveolar process. (tape)
32	Palatal length. Distance in the MSP between a tangent to the posterior borders of the medial incisor sockets and a tangent to the two curves in the posterior border of the palate.
33	Palatal breadth. Minimum distance between the borders of the canine sockets.
34	Palatal breadth. Minimum distance between the borders of the second premolar sockets.
35	Palatal breadth. Minimum distance between the borders of the second molar sockets.

CHEEK REGION

36	Number of infraorbital foramina.

TABLE 3.3- Continued

37	Minimum distance between the lateral border of the orbit and the outer border of the postorbital bar.
38	Minimum distance between the lower border of the orbit and the lower border of the zygomatic process of the maxilla.
39	Length of attachment of the superficial portion of the masseter. Minimum distance between the most anterior and the most posterior points of attachment.
40	Length and curvature of the zygomatic arch. From the most anterior point of attachment of the superficial masseter to the lowest point on the articular eminence. (tape)
41	Length and curvature of the zygomatic arch. Minimum distance between the most anterior point of attachment of the superficial masseter and the lowest point on the articular eminence.
42	Proportions of the zygomatic arch. Minimum distance between the most anterior point of attachment of the superficial masseter and the vertical projection onto the lower border of the zygomatic arch of the posterior border of the postorbital bar.
43	Minimum vertical thickness of the zygomatic arch.
44	Angle between the posterior border of the postorbital bar and the upper border of the zygomatic arch.
ARTICULAR REGION	
45	Development of the postglencid tubercle. Vertical distance from the lowest point on the postglenoid tubercle to the level of the highest point in the articular fossa.
46	Development of the medial border of the articular fossa. Vertical distance from the lowest point on the medial border to the level of the highest point in the fossa.
47	Development of the articular eminence. Vertical distance from the lowest point on the articular eminence to the level of the highest point in the fossa.

TABLE 3.3 - Continued

48	Shape of the articular fossa. Distance from the lowest point on the postglenoid tubercle to the most posterior point on the anterior edge of the articular area, on the surface of the fossa. (tape)
49	Shape of the articular fossa. Minimum distance between the lowest point on the postglenoid tubercle and the most posterior point on the anterior edge of the articular area.
50	Depth of the tympanic plate. Vertical distance from the lowest point on the tympanic plate to the level of the highest point in the articular fossa.
CALVARIUM	
51	Length. From the point of inflection behind the supraorbital torus to the most distant point on the braincase (excluding the occipital crest, if present).
52	Height. Vertical height from basion to the level of the highest point on the braincase (excluding the sagittal crest, if present).
53	Breadth. Maximum breadth above the buttress of the zygomatic process of the temporal bone.
54	Shape of the frontal eminence. Distance between the point of inflection behind the supraorbital torus and bregma. (tape)
55	Shape of the frontal eminence. Minimum distance between the point of inflection behind the supraorbital torus and bregma.
56	Postorbital constriction. Minimum breadth of the braincase at the level of glabella.
57	Conformation of bones at pterion. Length of the suture between sphenoid and parietal (+) or between frontal and temporal (-).
TEMPORAL REGION	
58	Vertical distance from porion to the temporal-parietal suture. (tape)
59	Vertical distance from porion to the top of the braincase. (tape)

TABLE 3.3- Continued

60	Vertical distance from porion to the top of the sagittal crest or the superior temporal line. (tape)
61	Distance from the postorbital point of attachment of temporalis along the superior temporal line to porion. (tape)
62	Length of the sagittal crest. Distance from the most anterior to the most posterior points. (tape)
OCCIPITAL REGION	
63	Development in the MSP. Distance over the surface of the occipital area from opisthion to the most distant point of attachment of the occipital musculature. (tape)
64	Development in the MSP. Minimum distance from opisthion to the most distant point of attachment of the occipital musculature.
65	Distance over the surface of the occipital area between the most lateral points of attachment of the occipital musculature. (tape)
66	Minimum distance between the most lateral points of attachment of the occipital musculature.
67	Development of the occipital crest. Distance in the MSP from basion to the point of maximum perpendicular projection of the braincase onto a line joining basion and the most distant point on the occipital crest.
68	Development of the occipital crest. Distance in the MSP from basion to the most distant point on the occipital crest.
69	Development of the occipital crest away from the MSP. Maximum distance, not in the MSP, from basion to the border of the occipital crest.
70	Development of the occipital crest away from the MSP. Distance from the surface of the braincase to the border of the occipital crest on its temporal side.
71	Angle between the MSP and a line passing through basion and the most distant point, not in the MSP, on the border of the occipital crest.

TABLE 3.3- Continued

FORAMEN MAGNUM

72 Maximum length in the MSP.

73 Maximum breadth perpendicular to the MSP.

74 Horizontal distance in the MSP between a line through the lowest points on the condyles and the vertical projection of the most posterior point on the braincase (excluding crests, if present).

75 Distance in the MSP from a line through the lowest points on the condyles to alveolare.

MASTOID PROCESS

76 Degree of development of the mastoid process (ranked 0 - 10).

TYMPANIC REGION

77 Angle between the axis of the external auditory meatus and the long axis of the petrous portion of the temporal bone.

BASICRANIAL STRUT

78 Distance in the MSP from basion to the sphenoid-vomer suture.

LOWER JAW

79 External symphysial angle. Angle in the MSP between the horizontal plane tangent to the base of the mandible and a plane tangent to the anterior surface of the symphysis.

80 Internal symphysial angle. Angle in the MSP between the horizontal plane tangent to the base of the mandible and a plane tangent to the posterior surface of the symphysis.

81 Curvature of the incisor row. Distance between the most posterior points on the borders of the lateral incisor sockets.

TABLE 3.3- Continued

82	Curvature of the incisor row. Distance in the MSP between a tangent to the posterior borders of the medial incisor sockets and a tangent to the posterior borders of the lateral incisor sockets.
83	Length of the incisor row. From the most medial point on the border of the medial incisor socket to the most lateral point on the border of the lateral incisor socket.
84	Distance between the most anterior and the most posterior points on the border of the medial incisor socket.
85	Length of the diastema. Minimum distance between the borders of the lateral incisor socket and the canine socket.
86	Maximum length of the canine socket.
87	Maximum width of the canine socket perpendicular to the maximum length.
88	Length of the premolar region. Distance between the most anterior point on the border of the first premolar socket and the most posterior point on the border of the second premolar socket.
89	Length of the molar region. Minimum distance between the most anterior point on the border of the first molar socket and the most posterior point on the border of the socket of the most posterior molar visible.
90	Distance between the most medial and the most lateral points on the border of the second molar socket.
91	Total length of the tooth row. Distance along the buccal surface of the alveolar process from its posterior margin to the highest point in the MSP between the medial incisors.
92	Total length of the tooth row. Distance along the lingual surface of the alveolar process from its posterior margin to the highest point in the MSP between the medial incisors.

TABLE 3.3- Continued

93	Palatal breadth. Minimum distance between the borders of the canine sockets.
94	Palatal breadth. Minimum distance between the borders of the second premolar sockets.
95	Palatal breadth. Minimum distance between the borders of the second molar sockets.
96	Distance between the most medial points on the articular heads of the condylar processes.
97	Distance between the most lateral points on the articular heads of the condylar processes.
98	Maximum perpendicular distance from the base of the mandibular notch to a plane tangential to the upper surfaces of the coronoid and condylar processes.
99	Angle in the ISP between the horizontal plane tangent to the base of the mandible and a plane tangent to the posterior borders of the angles of the mandible and the posterior surfaces of the articular heads of the condylar processes.

TABLE 3.4

CHARACTER VALUES FOR THE HOMINOID SKULLS*

Character Number	Skulls									
	1	2	3	4	5	6	7	8	9	10
1	25	19	20	13	32	20	9	5	10	0
2	27	24	18	13	45	29	12	5	12	0
3	16	16	21	18	37	27	11	4	13	11
4	101	76	123	108	162	125	86	57	93	80
5	90	69	114	100	137	104	79	58	80	72
6	38	33	44	41	41	40	32	32	29	27
7	40	35	38	38	46	37	32	27	31	28
8	9	3	8	10	nc	7	7	8	-3	nc
9	19	14	13	11	24	15	8	4	9	12
10	34	30	45	37	47	51	26	20	22	19
11	15	13	13	10	35	22	11	5	8	11
12	31	28	46	35	38	31	23	19	26	14
13	28	22	36	26	48	26	19	13	24	16
14	15	11	10	15	8	15	9	7	9	7
15	1	1	1	0	2	4	2	1	1	0
16	2	1	0	1	0	0	0	0	0	1
17	1	0	1	0	1	0	0	1	0	0
18	0	0	0	1	2	9	0	9	5	2
19	20	17	27	23	22	16	11	8	11	12
20	20	17	18	15	24	10	12	11	19	14
21	31	26	37	30	33	27	27	22	23	15
22	4	2	2	0	3	5	4	3	3	3
23	18	16	23	19	21	19	19	14	14	11
24	9	9	12	12	11	10	8	6	5	3
25	8	5	8	3	8	1	2	2	4	3
26	15	11	19	16	19	14	7	9	7	6
27	12	10	15	14	15	11	6	7	5	4
28	13	14	19	19	21	20	13	18	16	15
29	27	26	36	33	44	26	30	nc	25	13
30	12	11	13	13	16	14	14	nc	nc	nc
31	84	71	104	84	113	83	56	46	64	45
32	71	62	88	67	97	73	49	42	48	38
33	39	34	45	36	42	30	34	24	33	23

*All linear values in millimetres, nc = no comparison

TABLE 3.4- Continued

CHARACTER VALUES FOR THE HOMINOID SKULLS

Character Number	Skulls									
	1	2	3	4	5	6	7	8	9	10
34	41	35	46	41	34	31	28	24	30	23
35	38	36	44	39	36	27	26	nc	nc	nc
36	2	2	3	2	1	2	3	3	2	1
37	19	7	24	12	15	13	8	8	7	6
38	26	20	39	36	45	27	18	19	21	16
39	44	32	59	44	62	43	23	21	21	nc
40	70	53	115	73	88	65	50	34	40	nc
41	60	48	87	65	77	59	44	31	38	nc
42	16	10	19	17	24	18	8	3	3	nc
43	7	7	18	15	12	13	6	8	5	7
44	80	85	65	70	79	70	80	60	78	100
45	1	3	9	8	15	10	6	6	7	nc
46	9	7	16	11	18	12	10	7	6	nc
47	6	3	6	4	7	6	4	5	3	1
48	23	20	42	30	30	29	10	20	13	nc
49	20	18	38	27	28	24	10	15	13	nc
50	12	12	13	9	24	22	10	15	12	nc
51	112	120	116	122	149	121	108	101	113	123
52	92	90	104	102	106	92	79	82	86	77
53	96	98	94	103	104	97	95	88	99	97
54	54	63	59	64	69	67	55	62	57	66
55	52	60	57	61	63	65	51	56	53	58
56	65	70	67	69	72	67	65	60	72	68
57	-29	-9	-20	13	-20	-24	-16	-9	-8	nc
58	28	35	45	33	38	23	6	19	3	nc
59	99	102	100	110	108	94	93	100	96	95
60	84	68	112	96	124	77	56	44	54	nc
61	250	180	290	255	370	250	145	115	147	nc
62	nc	nc	70	nc	127	nc	nc	nc	nc	nc
63	53	47	70	51	100	56	40	32	45	nc
64	50	43	68	48	98	55	36	34	41	nc
65	129	140	165	145	175	126	116	102	122	nc
66	118	112	143	123	156	109	98	89	97	nc

TABLE 3.4- Continued

CHARACTER VALUES FOR THE HOMINOID SKULLS

Character Number	Skulls									
	1	2	3	4	5	6	7	8	9	10
67	72	71	88	82	85	74	62	76	68	nc
68	73	67	83	81	126	75	58	61	64	nc
69	74	nc	89	75	122	79	nc	nc	nc	nc
70	3	nc	16	5	33	6	nc	nc	nc	nc
71	25	nc	30	50	10	15	nc	nc	nc	nc
72	28	29	35	35	30	24	27	25	26	nc
73	23	25	28	26	28	26	21	22	nc	nc
74	31	42	27	31	44	40	43	35	56	nc
75	146	125	183	149	199	141	102	86	111	nc
76	0	0	0	0	3	1	3	0	2	nc
77	130	115	110	120	110	110	125	120	135	nc
78	46	44	56	47	64	51	33	35	35	nc
79	110	100	110	100	110	105	115	90	115	114
80	50	65	50	55	50	50	58	70	55	54
81	19	19	21	21	20	19	16	17	23	12
82	3	2	2	3	2	3	4	2	3	2
83	15	13	16	15	16	14	12	12	6	9
84	9	9	10	9	10	9	6	6	5	4
85	2	2	2	1	4	1	1	1	1	3
86	15	11	16	15	17	12	6	9	8	5
87	12	9	15	14	13	10	5	7	6	5
88	17	17	25	22	27	23	15	22	19	19
89	32	32	44	42	52	43	22	nc	28	16
90	11	9	13	11	13	12	7	nc	nc	nc
91	80	75	98	92	104	93	55	48	65	45
92	62	57	84	75	92	76	46	34	41	42
93	23	25	30	36	24	23	29	20	28	18
94	34	33	38	35	35	28	29	23	31	21
95	36	35	40	38	36	30	33	nc	nc	nc
96	65	61	75	68	72	57	49	49	50	52
97	111	98	144	129	139	107	83	76	80	80
98	11	12	10	20	20	14	9	7	8	6
99	125	140	110	100	60	115	65	50	63	70

TABLE 3.4- Continued

CHARACTER VALUES FOR THE HOMINOID SKULLS

Character Number	Skulls									
	11	12	13	14	15	16	17	18	19	20
1	nc	18	17	22	27	17	16	0	0	0
2	17	16	28	28	35	22	25	0	0	0
3	13	15	19	17	26	15	20	11	7	0
4	134	118	145	154	173	136	126	118	97	107
5	108	108	120	125	137	118	103	107	86	89
6	nc	32	33	38	40	nc	33	35	34	31
7	nc	39	44	47	50	42	39	40	35	33
8	nc	nc	nc	nc	nc	nc	nc	14	nc	9
9	nc	22	22	24	27	25	23	21	16	17
10	nc	nc	21	28	25	nc	19	21	16	19
11	nc	nc	nc	22	19	nc	nc	18	13	14
12	nc	28	31	39	34	nc	32	40	34	22
13	nc	30	30	35	31	nc	31	26	19	20
14	nc	nc	8	13	9	nc	10	9	6	1
15	nc	nc	4	4	5	nc	7	10	10	7
16	nc	nc	4	5	2	nc	nc	5	5	4
17	nc	nc	2	4	4	nc	nc	5	5	4
18	nc	nc	0	0	0	nc	0	0	0	1
19	16	12	8	7	7	nc	4	5	4	2
20	16	19	26	27	34	nc	22	18	22	11
21	20	nc	17	21	25	21	23	22	17	18
22	1	nc	2	1	2	0	1	3	1	3
23	13	nc	15	14	17	15	18	14	12	13
24	nc	nc	9	9	8	8	7	7	6	8
25	nc	nc	0	0	1	2	0	2	2	1
26	nc	8	10	9	11	10	9	7	7	3
27	nc	7	8	8	8	7	7	5	5	3
28	16	18	14	15	16	14	14	11	10	13
29	36	42	32	34	31	30	30	18	17	20
30	16	16	13	11	13	10	11	10	10	nc
31	75	nc	62	75	74	71	nc	59	54	50
32	56	1	51	59	58	58	58	47	41	32
33	23	31	23	33	34	30	31	27	21	27

TABLE 3.4- Continued

CHARACTER VALUES FOR THE HOMINOID SKULLS

Character Number	Skulls									
	11	12	13	14	15	16	17	18	19	20
34	31	32	35	45	45	42	40	38	29	30
35	37	37	42	51	50	49	42	43	36	37
36	nc	1	1	2	1	nc	1	1	1	1
37	9	11	8	11	15	9	12	8	5	6
38	27	31	25	24	27	25	27	27	17	17
39	nc	nc	nc	40	41	35	nc	43	30	24
40	nc	79	57	68	55	53	58	61	46	46
41	nc	68	49	60	49	47	51	51	43	39
42	nc	24	15	23	33	12	15	22	14	12
43	nc	11	10	10	6	6	nc	4	5	4
44	nc	75	85	93	110	103	110	95	100	100
45	nc	7	nc	8	9	7	8	11	3	3
46	nc	12	15	9	6	8	6	7	nc	3
47	nc	nc	12	10	10	13	9	10	3	6
48	nc	23	22	22	19	21	19	30	14	20
49	nc	18	14	19	15	17	16	24	11	16
50	nc	23	23	16	19	22	17	26	nc	13
51	153	nc	186	205	205	186	182	175	162	170
52	83	82	101	126	131	129	106	145	117	nc
53	nc	107	142	160	147	145	133	156	135	122
54	47	nc	105	98	97	90	75	132	109	112
55	45	nc	96	89	94	85	72	119	102	94
56	nc	66	92	111	101	102	99	103	86	85
57	nc	nc	8	nc	nc	nc	nc	nc	nc	15
58	nc	nc	46	35	53	48	50	50	38	10
59	nc	90	138	161	152	161	142	179	150	145
60	nc	94	89	88	90	90	86	86	77	57
61	nc	nc	220	230	215	206	195	230	207	150
62	nc	51	nc	nc	nc	nc	nc	nc	nc	nc
63	nc	nc	65	57	60	63	nc	52	34	nc
64	nc	nc	62	54	59	53	nc	49	34	nc
65	nc	nc	109	122	167	156	nc	135	121	nc
66	nc	113	104	112	149	135	108	132	112	nc

TABLE 3.4- Continued

CHARACTER VALUES FOR THE HOMINOID SKULLS

Character Number	Skulls									
	11	12	13	14	15	16	17	18	19	20
67	nc	nc	92	114	113	113	94	129	nc	93
68	nc	nc	89	101	102	93	83	79	nc	62
69	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
70	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
71	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
72	nc	nc	nc	50	41	45	nc	36	31	nc
73	nc	nc	nc	36	28	28	nc	27	26	nc
74	60	nc	92	98	104	82	83	74	76	nc
75	143	nc	117	135	121	116	119	97	88	nc
76	4	3	6	8	8	9	5	10	10	8
77	nc	nc	nc	135	180	160	nc	180	nc	180
78	nc	44	nc	35	30	24	31	34	27	nc
79	100	nc	111	100	nc	88	nc	95	80	nc
80	70	nc	54	70	nc	70	nc	100	100	nc
81	10	nc	12	16	nc	17	nc	16	12	nc
82	2	nc	1	3	nc	0	nc	1	1	nc
83	8	nc	11	11	nc	11	nc	7	8	nc
84	6	nc	7	7	nc	6	nc	5	6	nc
85	0	nc	0	0	nc	0	nc	1	2	nc
86	9	nc	10	10	nc	9	nc	8	6	nc
87	6	nc	8	6	nc	7	nc	5	4	nc
88	19	nc	16	13	nc	12	nc	13	11	nc
89	48	nc	33	39	nc	36	nc	22	21	nc
90	15	nc	13	9	nc	11	nc	8	8	nc
91	90	nc	62	66	nc	65	nc	65	55	nc
92	71	nc	51	55	nc	52	nc	40	nc	nc
93	nc	nc	17	35	nc	26	nc	20	18	nc
94	nc	nc	32	40	nc	39	nc	35	30	nc
95	nc	nc	44	49	nc	46	nc	50	42	nc
96	nc	nc	85	93	nc	85	nc	86	71	nc
97	nc	nc	126	147	nc	133	nc	125	101	nc
98	11	nc	12	10	nc	13	nc	15	14	nc
99	60	nc	75	60	nc	80	nc	65	45	nc

TABLE 3.5

CALCULATION OF WEIGHTED AND UNWEIGHTED

SIMILARITY BETWEEN TWO GROUPS

i	j	w_i	w_j	S_{ij}	$w_i w_j$	$w_i w_j S_{ij}$
13	18	8	1	1.001	8	8.008
13	19	8	1	1.147	8	9.176
13	20	8	2	1.688	16	27.008
14	18	2	1	1.063	2	2.126
14	19	2	1	1.718	2	3.436
14	20	2	2	2.274	4	9.096
15	18	4	1	1.135	4	4.540
15	19	4	1	1.902	4	7.608
15	20	4	2	2.587	8	20.696
16	18	1	1	0.676	1	0.676
16	19	1	1	1.109	1	1.109
16	20	1	2	1.725	2	3.450
17	18	1	1	0.876	1	0.876
17	19	1	1	0.879	1	0.879
17	20	1	2	1.583	2	3.166
				21.363	64	101.850
				$\Sigma\Sigma_{ij} S_{ij}$	$\Sigma\Sigma_{ij} w_i w_j$	$\Sigma\Sigma_{ij} w_i w_j S_{ij}$

$S = 101.85 / 64 = 1.592$

$S' = 21.36 / 15 = 1.424$

TABLE 3.6

PRINCIPAL COMPONENTS ANALYSIS
OF HOMINOID CORRELATION COEFFICIENTS

Skull Number	Latent vectors			
	I	II	III	IV
1	0.674	- 0.076	- 0.462	- 0.117
2	0.574	- 0.303	- 0.508	- 0.106
3	0.739	0.270	- 0.369	0.246
4	0.660	0.169	- 0.387	0.233
5	0.590	0.536	0.052	- 0.004
6	0.753	0.010	0.187	0.088
7	0.457	- 0.518	0.161	- 0.323
8	0.352	- 0.641	0.250	0.253
9	0.330	- 0.587	0.146	- 0.503
10	0.073	- 0.637	0.431	- 0.148
11	0.115	0.673	0.544	- 0.066
12	0.382	0.589	0.627	- 0.046
13	- 0.640	0.328	0.286	- 0.071
14	- 0.723	0.178	- 0.234	- 0.216
15	- 0.731	0.194	- 0.198	- 0.368
16	- 0.862	0.180	- 0.341	0.000
17	- 0.753	0.122	- 0.221	- 0.367
18	- 0.814	- 0.200	0.008	0.406
19	- 0.807	- 0.272	0.019	0.303
20	- 0.697	- 0.497	0.220	0.246
Latent root	7.86	3.32	2.17	1.24
% Total variance	39.32	55.93	66.77	72.96

TABLE 3.7

PRINCIPAL COMPONENTS ANALYSIS
OF HOMINOID DISTANCE COEFFICIENTS

Skull Number	Latent vectors			
	I	II	III	IV
1	0.935	- 0.179	0.168	0.170
2	0.962	0.017	0.172	0.150
3	0.793	- 0.530	0.168	0.148
4	0.917	- 0.271	0.133	0.126
5	0.745	- 0.605	0.035	- 0.118
6	0.921	- 0.205	0.223	- 0.008
7	0.913	0.211	0.277	0.070
8	0.870	0.325	0.312	0.001
9	0.925	0.225	0.220	- 0.030
10	0.854	0.395	0.221	- 0.112
11	0.939	- 0.013	0.079	- 0.306
12	0.957	- 0.106	0.070	- 0.217
13	0.954	0.000	- 0.190	- 0.133
14	0.917	- 0.100	- 0.309	- 0.025
15	0.887	- 0.145	- 0.385	0.024
16	0.934	- 0.006	- 0.307	0.026
17	0.965	0.017	- 0.203	- 0.025
18	0.896	0.122	- 0.335	0.097
19	0.897	0.327	- 0.201	0.088
20	0.860	0.417	- 0.113	0.088
Latent root	16.34	1.49	1.02	0.31
% Total variance	81.70	89.15	94.23	95.77

TABLE 3.8

SIMILARITY VALUES

OF PAIRS OF HOMINOID SKULLS

Comparison Form	Form	Similarity coefficent*					
		n	r	cos θ	MSD	MCD	Shape
1	2	95	0.657	0.539	0.445	0.522	0.325
	3	98	0.587	0.535	1.210	0.893	0.766
	4	98	0.424	0.431	0.750	0.606	0.711
	5	96	0.317	0.305	2.093	1.175	1.267
	6	98	0.410	0.419	0.736	0.610	0.738
	7	95	0.318	0.148	1.212	0.933	0.690
	8	89	0.032	-0.090	1.996	1.224	1.129
	9	90	0.111	-0.030	1.408	0.983	0.875
	10	64	-0.011	-0.261	2.506	1.361	1.139
	11	42	-0.269	-0.307	1.718	1.127	1.580
	12	42	-0.013	0.005	0.948	0.797	0.971
	13	87	-0.503	-0.469	1.536	1.046	1.551
	14	93	-0.442	-0.320	1.809	1.090	1.733
	15	72	-0.355	-0.254	1.935	1.210	1.667
	16	80	-0.517	-0.475	1.796	1.175	1.814
	17	60	-0.398	-0.384	1.350	0.972	1.371
	18	94	-0.563	-0.532	2.343	1.300	2.368
	19	87	-0.516	-0.537	2.398	1.361	2.025
	20	63	-0.523	-0.506	2.801	1.354	2.563
2	3	95	0.378	0.042	2.030	1.165	1.027
	4	95	0.457	0.245	0.853	0.767	0.554
	5	94	0.112	-0.205	2.959	1.437	1.384
	6	95	0.304	0.188	0.895	0.753	0.725
	7	95	0.300	0.484	0.677	0.689	0.541
	8	89	0.179	0.395	1.078	0.860	0.745
	9	90	0.266	0.443	0.677	0.650	0.538
	10	64	0.085	0.216	1.435	0.973	0.822
	11	42	-0.356	-0.307	1.354	0.933	1.385
	12	42	-0.214	-0.272	1.054	0.824	0.859
	13	87	-0.527	-0.533	1.303	0.943	1.222
	14	93	-0.421	-0.532	1.782	1.085	1.354
	15	72	-0.398	-0.605	2.093	1.208	1.240

* See Table 2.1 for formulae of similarity coefficients

TABLE 3.8 -- Continued

Comparison Form	Form	Similarity coefficient					
		n	r	cos θ	MSD	MCD	Shape
2	16	80	-0.363	-0.413	1.433	0.994	1.277
	17	60	-0.324	-0.324	0.973	0.831	0.840
	18	94	-0.498	-0.504	1.990	1.211	1.873
	19	87	-0.334	-0.112	1.483	1.037	1.429
	20	63	-0.404	-0.028	1.769	1.033	1.789
3	4	98	0.667	0.707	0.849	0.726	0.647
	5	97	0.541	0.711	1.143	0.823	1.085
	6	98	0.422	0.442	1.429	0.969	1.080
	7	95	0.065	-0.347	3.417	1.554	1.520
	8	89	0.019	-0.407	4.266	1.735	1.784
	9	90	-0.050	-0.424	3.596	1.590	1.700
	10	64	-0.288	-0.593	4.900	1.861	2.179
	11	42	-0.002	-0.113	2.569	1.329	1.660
	12	43	0.184	0.230	2.230	1.240	1.514
	13	87	-0.515	-0.340	2.934	1.450	2.466
	14	93	-0.428	-0.035	2.646	1.457	2.544
	15	72	-0.551	-0.053	3.029	1.519	3.044
	16	80	-0.489	-0.247	2.947	1.526	2.559
	17	60	-0.529	-0.386	2.986	1.447	2.489
	18	94	-0.567	-0.381	3.740	1.728	3.347
	19	87	-0.663	-0.743	4.847	1.986	3.199
	20	63	-0.656	-0.737	5.500	2.047	4.185
4	5	96	0.286	0.429	1.855	1.081	1.378
	6	98	0.379	0.411	0.851	0.645	0.839
	7	95	0.131	-0.143	1.813	1.140	0.961
	8	89	0.119	-0.178	2.366	1.335	1.116
	9	90	0.010	-0.239	1.934	1.149	1.080
	10	64	-0.338	-0.495	3.348	1.527	1.744
	11	42	0.049	-0.033	1.463	1.021	1.196
	12	42	0.089	0.144	0.935	0.773	0.919
	13	87	-0.492	-0.411	1.773	1.185	1.738
	14	93	-0.315	-0.109	1.703	1.131	1.704
	15	72	-0.494	-0.277	2.074	1.281	1.920
	16	80	-0.424	-0.308	1.759	1.185	1.761
	17	60	-0.477	-0.441	1.457	1.024	1.462

TABLE 3.8-- Continued

Comparison Form	Form	Similarity coefficient					
		n	r	cos θ	MSD	MCD	Shape
4	18	94	-0.550	-0.469	2.514	1.358	2.511
	19	87	-0.571	-0.639	2.844	1.523	2.229
	20	63	-0.538	-0.571	3.102	1.497	2.726
5	6	96	0.478	0.469	1.748	1.091	1.043
	7	94	-0.067	-0.500	4.479	1.830	1.772
	8	88	-0.216	-0.615	5.582	2.029	2.159
	9	89	-0.120	-0.542	4.456	1.828	1.769
	10	64	-0.171	-0.609	5.448	1.975	1.923
	11	42	0.247	0.026	2.854	1.425	1.252
	12	43	0.529	0.435	1.956	1.138	0.706
	13	87	-0.216	-0.067	2.784	1.435	1.957
	14	93	-0.462	0.029	2.999	1.563	2.647
	15	72	-0.277	0.250	2.613	1.442	2.414
	16	80	-0.459	-0.148	3.333	1.678	2.491
	17	60	-0.388	-0.199	2.951	1.522	1.948
	18	93	-0.544	-0.308	4.182	1.813	3.346
	19	87	-0.573	-0.680	5.313	2.047	3.055
	20	62	-0.694	-0.772	5.993	2.131	3.980
6	7	95	0.302	0.084	1.437	1.004	0.809
	8	89	0.374	0.069	1.798	1.145	0.773
	9	90	0.177	-0.044	1.537	1.053	0.881
	10	64	0.051	-0.224	2.636	1.421	1.199
	11	42	0.110	0.035	1.302	0.956	1.109
	12	42	0.320	0.345	0.692	0.688	0.705
	13	87	-0.364	-0.328	1.606	1.094	1.616
	14	93	-0.576	-0.397	2.161	1.205	2.129
	15	72	-0.582	-0.354	2.351	1.285	2.199
	16	80	-0.723	-0.655	2.079	1.249	2.104
	17	60	-0.551	-0.510	1.663	1.057	1.665
	18	94	-0.570	-0.524	2.607	1.385	2.631
	19	87	-0.600	-0.623	2.817	1.507	2.387
	20	63	-0.492	-0.520	3.115	1.485	2.769
7	8	89	0.416	0.706	0.628	0.599	0.595
	9	90	0.554	0.760	0.379	0.425	0.383
	10	64	0.266	0.584	0.938	0.720	0.767

TABLE 3.8— Continued

Comparison Form	Form	Similarity coefficient					
		n	r	cos θ	MSD	MCD	Shape
7	11	42	-0.195	-0.070	1.552	1.029	1.486
	12	42	0.054	-0.093	1.429	0.974	0.796
	13	87	-0.400	-0.382	1.888	1.155	1.406
	14	93	-0.289	-0.504	2.582	1.353	1.487
	15	72	-0.397	-0.651	3.110	1.499	1.525
	16	80	-0.559	-0.544	2.413	1.291	1.746
	17	60	-0.364	-0.331	1.608	1.088	1.146
	18	94	-0.365	-0.355	2.555	1.303	2.020
	19	87	-0.286	0.109	1.681	1.030	1.681
	20	63	-0.057	0.292	1.640	0.939	1.623
8	9	88	0.412	0.706	0.630	0.619	0.598
	10	62	0.331	0.676	0.829	0.677	0.823
	11	37	-0.294	0.134	1.325	0.934	1.174
	12	39	-0.147	-0.159	2.069	1.182	1.091
	13	81	-0.316	-0.285	2.241	1.285	1.487
	14	87	-0.412	-0.594	3.282	1.535	1.734
	15	69	-0.503	-0.712	4.041	1.747	1.918
	16	74	-0.450	-0.429	2.598	1.367	1.509
	17	57	-0.465	-0.397	2.296	1.298	1.495
	18	88	-0.168	-0.240	2.742	1.400	1.801
	19	81	-0.121	0.237	1.722	1.114	1.593
	20	61	0.075	0.371	1.774	0.994	1.662
9	10	64	0.405	0.674	0.754	0.660	0.581
	11	39	-0.169	0.031	1.053	0.781	1.057
	12	40	-0.199	-0.229	1.314	0.902	0.743
	13	83	-0.388	-0.351	1.685	1.111	1.277
	14	88	-0.236	-0.476	2.198	1.267	1.223
	15	69	-0.260	-0.591	2.749	1.433	1.213
	16	75	-0.385	-0.414	2.006	1.213	1.403
	17	58	-0.250	-0.248	1.335	1.011	0.850
	18	89	-0.326	-0.330	2.394	1.233	1.863
	19	82	-0.310	0.091	1.615	1.054	1.624
	20	62	-0.038	0.330	1.560	0.943	1.528
10	11	36	-0.202	0.129	1.684	1.038	1.371
	12	28	-0.147	-0.010	1.841	1.127	0.898

TABLE 3.8-- Continued

Comparison Form	Form	Similarity coefficient					
		n	r	cos θ	MSD	MCD	Shape
10	13	63	-0.143	-0.113	2.097	1.232	1.226
	14	64	-0.358	-0.563	3.441	1.658	1.654
	15	45	-0.193	-0.597	3.798	1.728	1.295
	16	51	-0.418	-0.381	2.930	1.517	1.846
	17	40	-0.125	-0.237	2.199	1.351	0.975
	18	64	-0.012	-0.009	2.516	1.267	1.699
	19	63	0.088	0.366	1.628	0.971	1.424
	20	44	0.310	0.556	1.088	0.835	0.916
11	12	17	0.766	0.734	0.233	0.368	0.203
	13	42	0.195	0.194	0.911	0.806	0.916
	14	42	-0.024	-0.065	1.356	0.899	1.289
	15	26	-0.158	-0.278	2.158	1.284	1.327
	16	40	-0.025	-0.010	1.274	0.898	1.303
	17	25	-0.196	-0.238	0.987	0.832	0.943
	18	42	-0.342	-0.294	2.221	1.176	2.266
	19	41	-0.195	-0.051	2.098	1.215	1.895
	20	22	-0.390	-0.102	2.498	1.105	2.585
12	13	40	0.132	0.167	0.707	0.710	0.725
	14	42	-0.365	-0.180	1.361	0.933	1.241
	15	42	-0.231	-0.083	1.783	1.178	1.554
	16	36	-0.569	-0.444	1.541	0.996	1.584
	17	41	-0.277	-0.254	0.960	0.750	0.981
	18	42	-0.401	-0.380	1.851	1.093	1.891
	19	40	-0.510	-0.480	1.920	1.228	1.473
	20	38	-0.336	-0.352	2.367	1.223	1.784
13	14	86	0.489	0.484	0.671	0.632	0.578
	15	65	0.427	0.469	0.876	0.693	0.686
	16	74	0.488	0.503	0.584	0.558	0.587
	17	58	0.499	0.509	0.426	0.469	0.426
	18	86	0.372	0.378	1.001	0.813	1.013
	19	81	0.361	0.292	1.147	0.880	0.891
	20	58	0.326	0.136	1.688	0.957	1.284
14	15	72	0.561	0.704	0.568	0.561	0.568
	16	80	0.655	0.671	0.514	0.532	0.470

TABLE 3.8-- Continued

Comparison Form	Form	Similarity values					
		n	r	cos θ	MSD	MCD	Shape
14	17	60	0.640	0.589	0.493	0.601	0.339
	18	93	0.437	0.439	1.063	0.836	0.973
	19	87	0.414	0.116	1.718	1.133	0.902
	20	61	0.300	-0.096	2.274	1.244	1.336
15	16	59	0.702	0.732	0.502	0.516	0.366
	17	60	0.689	0.615	0.679	0.610	0.392
	18	72	0.398	0.449	1.135	0.857	1.008
	19	67	0.399	0.047	1.902	1.166	0.886
	20	61	0.287	-0.099	2.587	1.242	1.490
16	17	50	0.723	0.729	0.306	0.456	0.286
	18	80	0.618	0.621	0.676	0.676	0.677
	19	74	0.565	0.369	1.109	0.918	0.620
	20	48	0.447	0.150	1.725	1.010	1.197
17	18	60	0.413	0.423	0.876	0.724	0.872
	19	56	0.476	0.371	0.879	0.785	0.606
	20	54	0.270	0.126	1.583	0.930	1.199
18	19	87	0.824	0.693	0.629	0.621	0.329
	20	62	0.730	0.471	1.389	0.868	0.868
19	20	56	0.746	0.786	0.714	0.491	0.718

TABLE 3.9

DIFFERENCES BETWEEN STANDARDIZED CHARACTER VALUES OF MALE AND FEMALE GORILLA SKULLS

Rank order	Character number	Difference
1	68	2.304
2	63	2.660
3	13	2.656
4	64	2.656
5	35	2.636
6	25	2.595
7	66	2.483
8	38	2.345
9	60	2.312
10	18	2.305
11	20	2.254
12	29	2.215
13	65	2.213
14	70	- 2.167
15	61	2.196
16	14	1.940
17	99	1.918
18	75	- 1.896
19	33	1.831
20	11	1.787

4 PHENETIC RELATIONSHIPS AMONG THE HOMINOID SKULLS

4.1 Introduction

In the previous chapter, five methods of measuring overall resemblance were discussed and comparions were made between the patterns of relationship revealed by the five methods. These comparions were based on a series of hominoid skulls. The purpose of this chapter is to summarise the common features of these patterns of relationship and to compare the information these provide about phenetic relationships with intuitive assessments of morphological resemblance and with information provided by other taxonomic characters. The use of quantitative methods in investigating the relationships among fossil forms is also discussed.

4.2 Phenetic relationships among the Modern Groups

When the patterns of relationships of the four modern groups shown by the different methods are compared, the most striking feature they have in common is the clear separation between the three pongid groups and the Homo sapiens group (see Fig. 3.9, p. 86). This division agrees with that arrived at by intuitive assessments of differences between the skulls of members of these groups and has the advantage

of expressing the difference in quantitative terms. The features which distinguish the skull of Homo sapiens from those of the pongids are related to the much greater size of the brain case, which is combined with a vertical forehead and a rounded and backwardly projecting occipital region, the greatly reduced size of the jaws and teeth, and the position of the head which, in correlation with the erect posture, is balanced more evenly on the top of the vertical vertebral column (Le Gros Clark, 1959, p.159).

The patterns of relationship within the pongid group, on the other hand, show less agreement with intuitive assessments of differences between the skulls. The isolated position of the male orang and gorilla shown by the distance coefficients has already been discussed in Section 3.5 and is attributed to the sensitivity of these coefficients to size differences. However, all coefficients show less difference between the skull of the chimpanzee and that of the orang than between the skull of the chimpanzee and that of the gorilla, whereas an intuitive assessment of the differences between the skulls suggests the reverse. To the eye, the skulls of the chimpanzee and gorilla show a greater resemblance to each other than to that of the orang. For example, in the skulls of the chimpanzee and gorilla, the orbits are surmounted by a powerfully contructed

continuous transverse ridge, the supraorbital torus. In the skull of the orang, a continuous torus is absent and the forehead has a more rounded appearance. When making visual comparisons, however, there is a tendency to give greater weight to more obvious differences and it is difficult to give equal and simultaneous consideration to all features of the skulls which vary. For this reason, lack of agreement between the results of the quantitative methods and intuitive assessments of resemblance need not imply that the quantitative methods have failed to measure the overall resemblance of the skulls.

What evidence about phenetic relationships of the pongids is provided by other taxonomic characters? In terms of their post-cranial morphology, the chimpanzee and gorilla appear more similar to each other than to the orang and this is thought to reflect the partial abandonment of active brachiation by the African apes. Studies of biochemical characters also point to a closer similarity between the chimpanzee and gorilla. Goodman, for instance, studied the serum proteins of the apes by electrophoretic and serological techniques and found a greater similarity between the serum proteins of the chimpanzee and gorilla than between these and the orang. A similar pattern of similarities has been found in studies of chromosome morphology and of the peptide

composition of the haemoglobins of the apes. Although the similarities based on these characters have not been expressed in quantitative terms, they do suggest that there is a lack of agreement between the information provided by the skull characters used in this study and that provided by characters from other parts of the body and from other levels of biological organisation. Two interpretations of this lack of agreement can be put forward. The first is that the information provided by the skull characters is to some degree independent of that provided by other characters; the second is that the information provided by the particular skull characters used in this study is incomplete and that insufficient characters have been used. A study of the pattern of relationships using a larger number of characters would provide evidence with which to decide between these interpretations. Such a study has not yet been carried out but a comparison between the pattern of relationships based on 85 characters and that based on 99 characters can be made. In order to investigate the effects of standardisation (Section 3.6), correlations between skulls were calculated using only the 85 characters measured in the same unit. A comparison between the dendrogram based on 85 (standardised) characters (Fig. 3.10a) and that based on 99 (standardised) characters (Fig. 3.9a) shows that the addition of 14 characters has only

a small effect on the overall pattern of relationships and almost no effect upon the similarities of the pongid group. Although the difference in the number of characters is small, this comparison does suggest that the measurements of the similarities between the skulls have reached stable values, and would not alter, if based on yet more characters, sufficiently to reverse the pattern of relationships of the pongids.

It seems probable, therefore, that the coefficients of similarity are measuring the overall resemblance of the skulls. The first of the two interpretations is therefore the more probable one, that is, the information about phenetic relationships provided by skull characters is to some degree independent of that provided by other morphological characters or characters from other levels of organisation. This interpretation is supported by the observation that evolutionary changes in one part of the body or at one level of organisation are not necessarily accompanied by changes in other parts of the body or at other levels of organisation.

In addition to providing information about the phenetic relationships of the skulls of the modern forms, the results of the quantitative methods give clear indications of the relative effects of differences in sex and age on the skulls within each of the modern groups. In the dendrogram based on the correlation coefficient (Fig. 3.9 a), for example, the

gorilla skull shows a higher degree of sexual dimorphism than do the skulls of the chimpanzee or orang, and the sexual dimorphism shown by these is, in turn greater than that shown by the skulls of Homo sapiens. The dendrograms also express in quantitative terms the differencesbetween the amount of morphological change which takes place during development in the pongids and that which takes place in H.sapiens. The amount of change is much greater in the pongids than in H. sapiens and is sufficiently great to isolate the juvenile apes in a separate cluster. The difference in the amount of change between the pongids and H. sapiens, and the greater similarity between the juvenile sapiens and the juvenile apes (see, for example, Fig. 3.5 a) supports Schultz's conclusion that the differences in the Hominoidea become very marked only during growth (Schultz, 1963, p.107).

4.3 Phenetic relationships among the fossil forms

The purpose of this section is to summarise the information provided by the quantitative methods about the phenetic relationships of the fossil skulls and to discuss briefly the implications of this information. The fossil forms considered here are believed, by the majority of workers, to be members of populations lying on or near to the evolutionary line leading to modern man (a detailed account of the evidence for this

view is given by Le Gros Clark, 1955) and this assumption is used as a basis for the following discussion. The members of this evolutionary line constitute the family Hominidae. They are divided, on the basis of major gaps in the fossil record and corresponding morphological discontinuities, into two genera: Australopithecus and Homo; each of these is divided into two species; Australopithecus into africanus and robustus and Homo into erectus and sapiens (Campbell, 1963)

The most marked evolutionary changes which have occured within the hominid line are an increase in the size of the brain, a reduction in the size of the jaws and teeth and changes in the skeleton in response to the gradual adoption of a bipedal mode of progression. Although the adoption of bipedal progression is thought to have been associated with the initial divergence of the pongid and hominid lines, the changes in the relative sizes of the jaws, teeth and brain are thought to have occured only in the terminal phases of hominid evolution. The evidence for this view is provided by the Australopithecines which combine a skeleton clearly adapted for bipedal progression with a skull which has a small brain case and large jaws. The small brain case and large jaws give the skulls of the Australopithecines an overall ape-like appearance. The results of the quantitative methods agree with this intuitive assessment of the Australopithecine

skull. The Australopithecines are represented in this study by adult skulls from Sterkfontein and Swartkrans (11, 12) and the juvenile skull from Taung (10). In the dendrograms (Figs. 3.8, 3.9, pp.85, 86) and in the projections produced by principal components analysis (Figs. 3.4, 3.6, pp.71, 80), the Australopithecine skulls, adult and juvenile, show a greater similarity to the skulls of the modern pongids than to those of modern man.

The known Australopithecines fall into two main groups. One group, the africanus group (represented here by the skulls from Taung and Sterkfontein) contains small, generalised, light-framed forms; the other group, the robustus group (represented here by the skull from Swartkrans), contains larger, more dentally-specialised, robust forms. The morphological similarity between these groups when measured by quantitative methods shows some variation according to the particular similarity coefficient used. All methods, however, show that the morphological divergence between the groups (in so far as the skulls considered here are representative of the groups) is small, less, for example, than that shown by the fossil members of Homo sapiens (forms 14–17) and this result lends support to the modern view that the difference between the groups are not sufficient to justify their separation into different genera.

The members of Homo erectus are considered, in their morphological status, to be intermediate between the members of Australopithecus on the one hand and the members of Homo sapiens on the other. Their similarity with the members of H. sapiens is considered sufficient to justify their inclusion in the same genus. Homo erectus is represented in this study by a single skull, that of "Pekin" man (13) from Choukoutien. Its position, when judged by quantitative methods, varies according to the similarity coefficient used. When similarity is measured by the two angular coefficients or Penrose's shape coefficient, the Pekin skull lies outside the cluster of skulls of the fossil members of H. sapiens. When similarity is measured by distance coefficients, the skull lies within this cluster. The results produced by the first three coefficients are thus more in agreement with current opinions of the morphological status of the Pekin skull.

The position of this skull with respect to the Australopithecine skulls cannot be determined from the dendrograms since these only provide information about its similarity with the Australopithecine-ape cluster. In the projections obtained by principal components analysis, however, its position is clearly shown. It lies between the Australopithecines and the fossil sapiens forms and is slightly nearer the latter. The distances between the Pekin skull

and the Australopithecus and Homo sapiens groups are larger than those between forms within each of these groups. These "morphological gaps" correspond to the existing main taxonomic divisions within the hominid line and although they would probably be reduced if all the available fossil forms were included in the analysis, their size suggests that the existing taxonomic divisions reflect (as they are intended to) regions of marked morphological discontinuity.

The final stage in the evolutionary line leading to modern man consists of the fossil and modern populations which make up the species of Homo sapiens. The evolutionary relationships of these population are not yet fully understood and numerous evolutionary schemes have been put forward which try to account for the morphological, distributional and temporal characteristics of these populations. Weiner and Campbell have examined a number of hypotheses and suggest that a "spectrum" hypothesis is most in accordance with the available evidence. They suggest that the simplest hypothesis which accounts for the high degree of morphological continuity between the fossil populations which has been maintained in time and space is a simple radial deployment of populations characterised by a reticulate type of evolution. Weiner and Campbell suggest that the H. erectus stage was followed, 200,000 or 300,000 years ago, by a spectrum of varieties of

early H. sapiens ranging from pre-Solo, pre-Rhodesian and pre-Neanderthal groups to groups represented by Steinheim and Swanscombe Man which show many points of similarity with modern H. sapiens. Some of these populations continually intergraded and others were subjected to a high degree of isolation by climatic and other factors. In this way the spectrum broadened and towards the upper Pleistocene distinctive populations of Solo, Neanderthal and Rhodesian Man came into existence with "intermediate" populations such as those of Mt. Carmel and populations indistinguishable from those of modern H. sapiens. Weiner and Campbell consider that the degree of inter-relatedness implied in the "spectrum" hypothesis, in contrast to earlier theories, is such that it is not possible to maintain in a taxonomic sense strict specific status for the populations of Solo, Rhodesian, Neanderthal and modern H. sapiens (Weiner and Campbell, 1964, pp.205-207).

The four fossil H. sapiens skulls considered here are the skulls from La Chapelle (14) and Broken Hill (15) which belong to the distinctive Neanderthal and Rhodesian populations of the upper Pleistocene, the skull number 5 from the Skūhl cave at Mt. Carmel (16) which belongs to a population that appears to be morphologically intermediate between the Neanderthals and modern H. sapiens, and the skull

from Steinheim (17) which belongs to an early (second interglacial) population and which has a number of features in common with that of modern H. sapiens.

When the overall resemblance of these skulls is expressed in quantitative terms, they show a high degree of similarity to one another and form a tight cluster quite separate from the modern H. sapiens skulls. The pattern of relationships within the cluster and the relationship between it and the Pekin skull varies according to the coefficient used to measure resemblance. In the dendrograms based on the correlation coefficient and Penrose's shape coefficient (Fig. 3.9, a,c), the most similar skulls are those from Skuhl (16) and Steinheim (17) with the skulls from Broken Hill (15), La Chapelle (14) and Pekin (13) at successively greater distances from this nucleus. In the dendrograms based on the mean square distance and the mean character difference (Fig. 3.9, b,d), the most similar skulls are again those from Skuhl and Steinheim. However, in the mean square distance dendrogram , the Broken Hill skull (15) lies further from the nucleus than the Pekin skull and in the mean character difference dendrogram, both the Broken Hill and La Chapelle skulls lie further from the nucleus than the Pekin skull. Finally, in the dendrogram based on the cosine of the angle (Fig. 3.9, b), the most similar skulls

are those from Skūhl and Broken Hill with the skulls from La Chapelle, Steinheim and Pekin at successively greater distances from the nucleus of the cluster.

Of the five coefficients, the two angular coefficients and Penrose's shape coefficient produce patterns of relationship most similar to those based on intuitive assessments of morphological resemblance since they place the Pekin skull outside the cluster of fossil H. sapiens skulls. It is less easy, however, to decide whether the correlation coefficient and the shape coefficient, on the one hand, or the cosine of the angle, on the other, gives a pattern more similar to that based on intuitive assessments. The first two coefficients place the Steinheim skull inside the cluster, close to the Skūhl skull, whereas the third coefficient places it outside the cluster. Much of the Steinheim skull is missing but in terms of those features which are present it shows more similarity to the Skūhl skull than to the La Chapelle or Rhodesian skulls. In contrast with the latter skulls, the Skūhl and Steinheim skulls have braincases which are shorter and narrower but with laterally expanded walls and more highly arched foreheads. The supraorbital torus is less pronounced and the occipital region of the skull more rounded. The pattern based on the cosine of the angle thus shows less agreement with intuitive

assessments of resemblance than the patterns based on the correlation and shape coefficients.

The dendrograms provide less information about the relationships of the fossil forms than the projections obtained by principal components analysis since the dendrograms show mainly the relationships of the forms with the nucleus of the cluster of which they are members and provide little information about their inter-relationships with one another. In the projections obtained from a principal components analysis of correlations (Figs. 3.4, 3.5), the four fossil H. sapiens skulls form a cluster distinct from the modern H. sapiens and Pekin skulls. Within this cluster, the La Chapelle and Broken Hill skulls lie close to one another and in the direction of the Pekin skull. The Skuhl (16) and Steinheim (17) skulls lie in the direction of the modern H. sapiens skulls with the Steinheim skull nearer to the Skuhl skull to the La Chapelle and Broken Hill skulls. This distribution corresponds to some extent to the relative degrees to which these skulls show primitive and advanced features. The picture of the relationships of the fossil H. sapiens skulls produced by principal components analysis of correlations thus shows fairly good agreement with that suggested by Weiner and Campbell. The high degree of morphological similarity of the skull is clearly shown.

The Skuhl and Steinheim skulls have diverged more than the La Chapelle or Broken Hill skulls from the Pithecanthropine stage and lie in the direction of modern H. sapiens.

The main conclusions which can be drawn from this analysis of the relationships of the fossil skulls produced by quantitative methods are: firstly, that different pictures emerge depending upon the particular coefficient used to measure resemblance, and that of the five coefficients considered here, the correlation coefficient produces the picture which shows most agreement with intuitive ideas of the morphological resemblance of the fossil skulls; secondly, that the projections produced by principal components analysis provide more information about relationships than do the dendrograms produced by cluster analysis; thirdly, the agreement with intuitive ideas is sufficiently good to suggest that quantitative methods can provide a useful tool in the investigation of evolutionary relationships.

4.4 Summary

The purpose of this chapter has been to summarise the information provided by the quantitative methods about the phenetic relationships of the hominoid skulls. All methods point to a clear separation between the modern pongid and

and modern H. sapiens skulls. The pattern of relationships within the pongid group varies according to the coefficient used to measure similarity and the results of all methods show some lack of agreement with the evidence of other taxonomic characters. The quantitative methods give a clear indication of the relative effects of differences in sex and age. The pattern of relationship among the fossil skulls is in good agreement with intuitive assessments of overall resemblance.

5 PHENETIC RELATIONSHIPS AMONG RODENTS

5.1 Introduction

The purpose of this chapter is to present the results of a quantitative study of phenetic relationships among members of 21 genera of rodents. This study was undertaken to provide further evidence with which to judge the relative merits of different quantitative methods of analysing taxonomic relationships and to examine the kinds of taxonomic information provided by these.

The 21 genera were chosen from 7 families of rodents: the Heteromyidae, Zapodidae, Dipodidae, Cricetidae, Pedetidae, Geomyidae and Muridae. The first five families were chosen because they contain forms adapted to the same specialised mode of progression, leaping with the hind legs. Wood has suggested that this adaptation has arisen independently in each of the five families (Wood, 1947, p.159) and it is of interest, therefore, to see to what degree the similarities in functional adaptation between the members of these families are reflected in the patterns of relationship produced by quantitative methods. The sixth family, the Geomyidae, contains forms adapted to a burrowing way of life and these show a marked contrast in

their overall morphology to the members of the first five families. However, the Geomyidae are considered by rodent taxonomists to be very closely related, in a cladistic sense, to one of these families, the Heteromyidae, and were included in the analysis in order to see if the results of the quantitative methods provide any indication of this close relationship. The seventh family, the Muridae, were represented in this study by a single genus, Rattus. The members of this genus are unspecialised rodents and this genus was included in the analysis to provide a reference point by which to judge the degree of specialisation shown by members of the other families. Further information about the material studied and the families from which it was chosen is given in the next section.

5.2 Material and methods

The following information about the seven families from which the 21 genera were chosen is taken from Howell (1944) and Walker (1964).

1 Heteromyidae

This family consists of five genera. It occurs in Southwestern Canada, western United States and southward through Central America to Venezuela. Its habitats include prairies, deserts and dry, open forests (Perognathus,

Microdipodops, Dipodomys), bushy or grassy areas and humid tropical forests (Licmys, Heteromys). The heteromyids show considerable variation in their morphology. Licmys and Heteromys are generalised, mouse-like forms, Liomys is slightly saltatorial and Dipodomys and Microdipodops are highly saltatorial. These two genera show considerable inflation of the mastoid bullae, enlargement of the head and trunk, elongation of the tail, a relative reduction of the anterior limbs and elongation of the posterior limbs, partly by a lengthening of the metatarsals. All five genera were considered in this study and each genus was represented by a single species except Dipodomys which was represented by five species in order to give some indication of the degree of variation within a genus.

2 Zapodidae

This family consists of four genera and occurs in northern and eastern Europe and middle and eastern Asia (Sicista and Mozapus) and in Canada and the northern United States (Zapus and Napaeozapus). Its members inhabit forested areas, meadows and swamps. They are good leapers, except for the more generalised genus Sicista; but except for a long tail and somewhat elongated hind limbs they are not markedly modified for a jumping mode of progression. Three genera were considered here: Sicista, Zapus and Napaeozapus

and each was represented by a single species.

3 Dipodidae

This family consists of ten genera and inhabits northern Africa and southwestern Asia, through central Asia to northern China and southern Manchuria. Its members live in deserts, semi-desert areas and steppes. They are characterised by marked adaptation for jumping. The hind legs are at least four times longer than the front legs and are more protracted in relation to the front legs than in any other group of jumping rodents. Owing to a lack of available material, only two genera could be considered in this study. Alactaulus has five digits in the hind foot but the three metatarsals are fused to form a cannon bone. There is no enlargement of the bullae or fusion of the cervical vertebrae. The second genus, Jaculus, has only three digits in the hind foot. The metatarsals are fused to form a cannon bone, the bullae are inflated and the cervical vertebrae are fused together. Each genus was represented by a single species.

4 Cricetidae

This family consists of 100 genera and is nearly world-wide in its distribution. Only three of its genera were considered in this study. Gerbillus occurs in open, sandy and sparsely vegetated areas from southern Africa,

northward to Morocco and Egypt, eastward through Palestine and Arabia to West Pakistan, Tatera occurs in plains, savannahs and woodlands from Africa through southwestern Asia to India and Ceylon. Members of both genera adopt leaping modes of progression but their hind limbs and tails are not markedly elongated. The third genus, Leotoma, inhabits western and central North America southward to Guatemala. Its members are generalised rat-like forms and it was included for comparison with the two saltatorial genera. Each genus was represented by a single species.

5 Pedetidae

This family consists of a single genus, Pedetes, and inhabits dry, sandy soils in arid or semi-arid areas from east-central Africa southward to the Cape. Its members are of the size of small hares and show considerable adaptation to a leaping mode of progression. They resemble a large and clumsier version of Jaculus. The tail is long and the hind legs very long in proportion to the front legs but the bullae are not inflated, nor are the cervical vertebrae or metatarsals fused. The genus was represented by a single species.

6 Geomyidae

This family consists of eight genera and occurs only in North America. Its members are adapted to a burrowing

way of life and spend most of their life underground. They have stout, thickset bodies and the legs and tail are short. The forearms are powerful and have strong, digging claws. The skull is massive, angular, and flattened, with strong and widely flaring zygomatic arches. Six of the eight genera were considered in this study: Geomys, Thomomys, Cratogeomys, Orthogeomys, Heterogeomys and Zygogeomys. Each genus was represented by a single species.

7 Muridae

Of this family, only one genus Rattus, was considered in this study and was included to provide a reference point by which to judge the degree of specialisation shown by members of the other families.

The 25 species considered in this study are listed in Table 5.1. Whenever possible, each species was represented by four individuals but owing to a lack of available material, several species were represented by fewer individuals. The 25 species and the 64 individuals used to represent them were given reference numbers. These are shown in Table 5.1.

The material available for study consisted of skeletons and dried skins. A certain amount of information can be obtained from the skins - for example, the length of the external ear and the colour and distribution of pigmentation

but the skins tend to shrink and fade during the drying process and this information is therefore unreliable. For this reason, only the skeletons were considered in this study. An attempt was made to describe all features of the skeleton which varied over the 25 species and 244 characters were needed to do this. These are listed in Table 5.2. 231 of these characters were linear dimensions and were measured by sliding calipers to the nearest tenth of a millimetre. Certain characters of the vertebral column (178, 183, 187) were not measured. Their values are those published by Hatt (1932). The table of character values is too extensive to be given here but copies of this table are available.

The character values were standardised so that the values of each character had a mean of 1 and a standard deviation of 0. Three quantitative analyses of the relationships of the 64 forms were carried out. In two of the analyses, the similarities between the forms were measured by means of the correlation coefficient and the square root of the mean square distance coefficient. The resulting tables of similarity values were analysed by means of the unweighted average pair-group method of cluster analysis. In the third analysis, covariances between the characters used to describe the forms were calculated and the resulting table of covariances analysed by means of

principal components analysis. The first three latent vectors of the covariance table were extracted and the projections of the 64 forms onto each of these vectors were obtained. The tables of similarity values and projections are too extensive to be given here but copies of these are available.

5.3 Results

The results of the quantitative analyses are presented in Figs. 5.1 - 5.5.

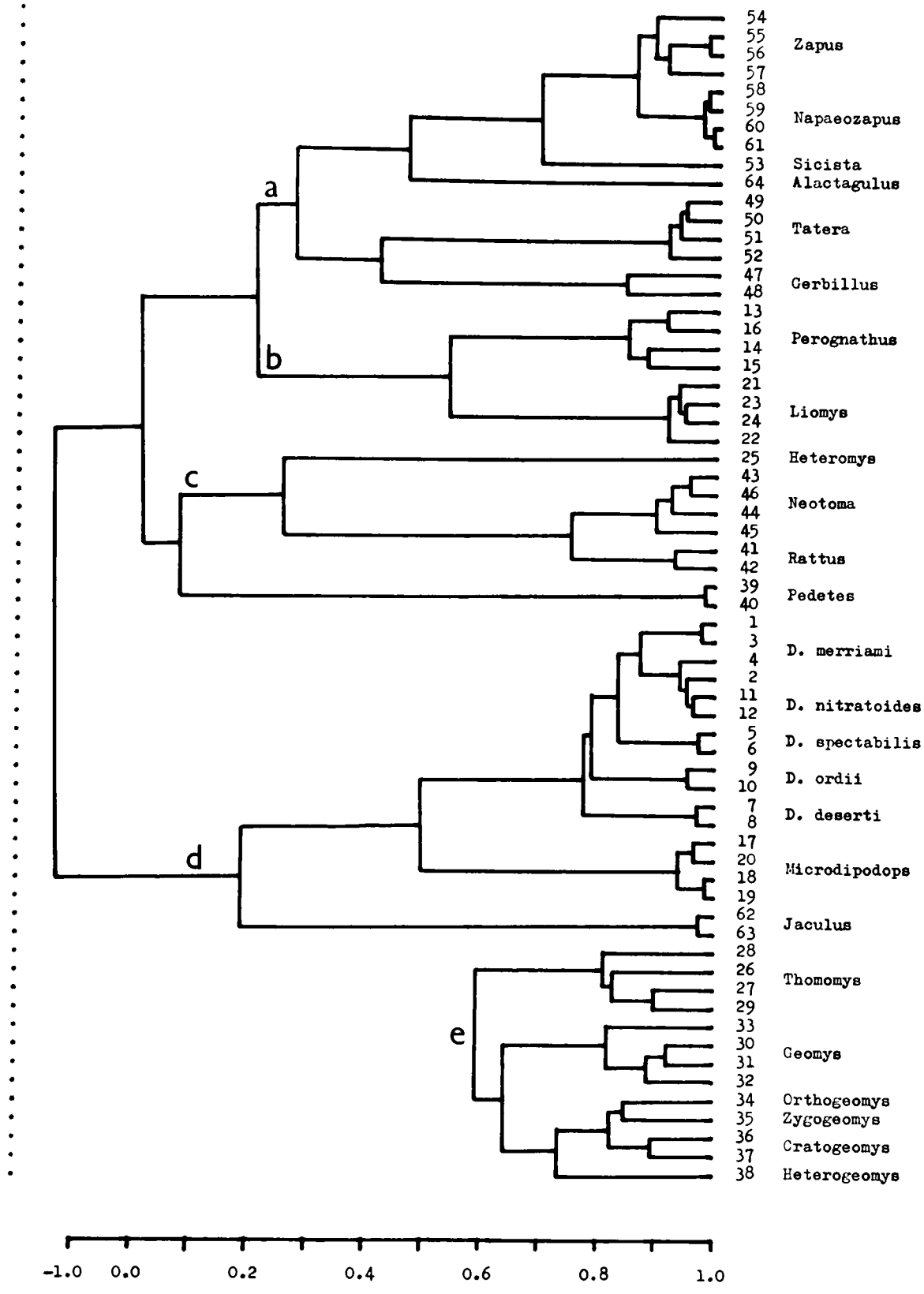
1. Cluster analysis of correlations between forms

The dendrogram produced by the cluster analysis of correlations between the 64 forms is shown in Fig. 5.1. The 64 forms show a clear separation into the 25 species with the exception of 2 of the 4 members of Dipodomys merriami (forms 1-4) which link with the 2 members of D. nitratoides (forms 11, 12). This separation suggests that each species (with the exception of D. merriami / D. nitratoides) is a distinct phenetic unit. The amount of morphological diversity within each species, however, varies considerably from species to species. Only in the case of Dipodomys can a measure of diversity between species within a genus be obtained. This diversity is quite large and is greater than that shown between several of the species belonging to different genera. Those variations in diversity clearly

Figure 5.1

Dendrogram produced by unweighted average pair-group cluster analysis of correlations between rodents. Correlations based on standardised character values.

The average correlation between the Geomyidae (forms 26-30) and the other forms is -0.264.


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10
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8
17
20
18
19
62
63
28
26
27
29
33
30
31
32
34
35
36
37
38
Zapus
Napaeozapus
Sicista
Alactagulus
Tatera
Gerbillus
Perognathus
Liomys
Heteromys
Neotoma
Rattus
Pedetes
D. merriami
D. nitratoides
D. spectabilis
D. ordii
D. deserti
Microdipodops
Jaculus
Thomomys
Geomys
Orthogeomys
Zygogeomys
Cratogeomys
Heterogeomys
a
b
c
d
e
-1.0
0.0
0.2
0.4
0.6
0.8
1.0

illustrate that the taxonomic categories of genus and species are not based on fixed amounts of morphological diversity.

The 25 species do not show a clear separation into families. Only the Zapodidae (forms 53-61) and the Geomyidae (forms 26-30) emerge as discrete clusters. The Heteromyidae are split into three parts: Dipodomys and Microdipodops form one group which links with Jaculus; Perognathus and Liomys form a second group which links with the Zapodidae - Alactaqulus - Tatera - Gerbillus group and Heteromys links with the Rattus - Neotoma group. The Dipodidae are split into two parts: Alactaqulus links with the Zapodidae and Jaculus with the Microdipodops - Dipodomys group. The Cricetidae are split into two parts: Tatera and Gerbillus link with the Zapodidae - Alactaqulus group and Neotoma links with Rattus. The main clusters which do emerge can, however, be interpreted in terms of the differences in functional adaptation shown by the 25 species. Cluster e (see fig. 5.1) corresponds to the Geomyidae, all members of which show marked adaptation to a burrowing way of life. The clear separation between these and the other forms suggests that this adaptation pervades the whole skeleton.

The remaining forms, with the exception of Pedetes, fall into 4 main clusters. Cluster a contains the Zapodidae, Alactaqulus and the two gerbils Tatera and Gerbillus. The

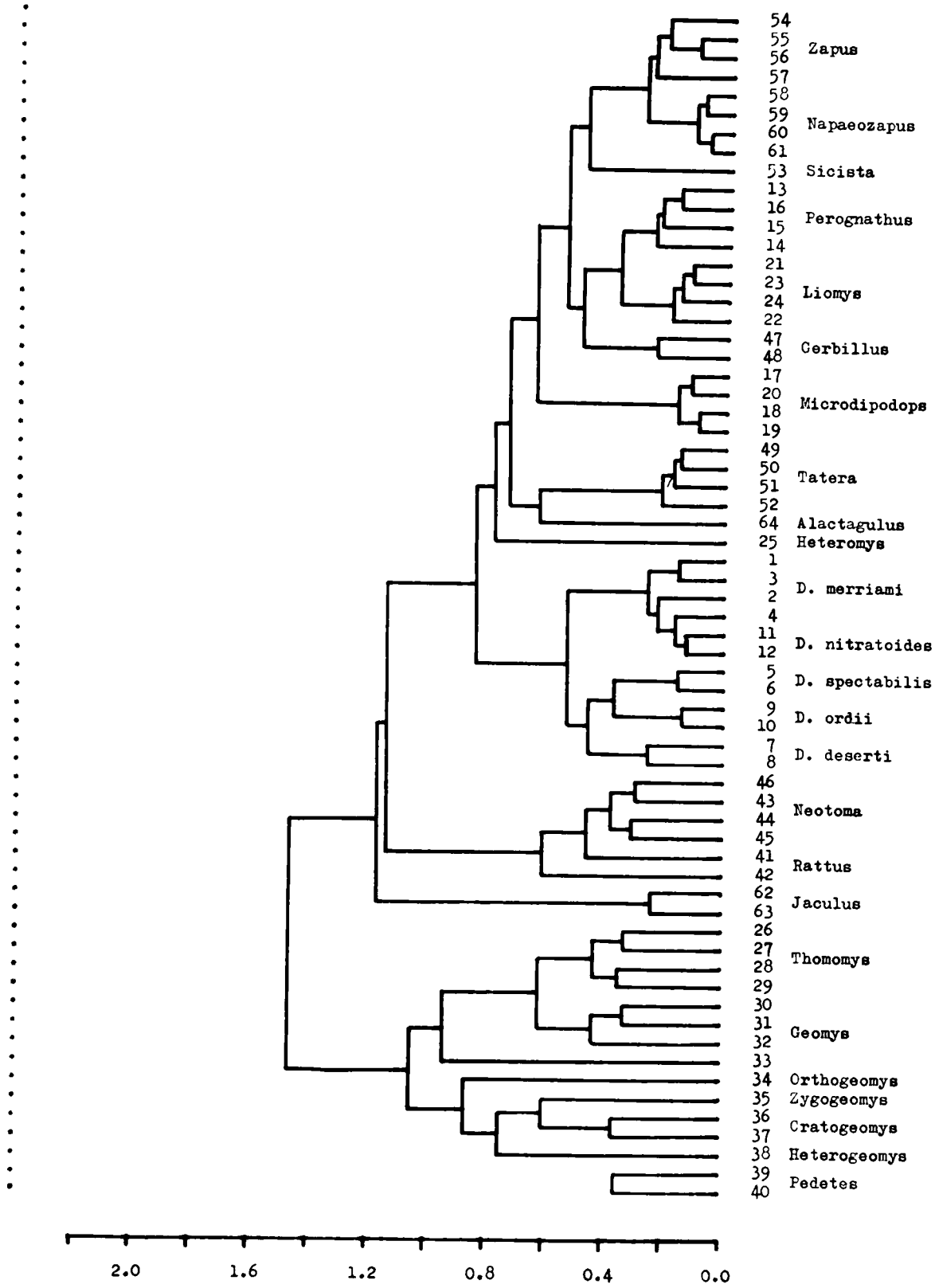
members of these genera are saltatorial forms and show a relative elongation of the hind legs and tail. They do not, however, show inflation of the bullae, fusion of the cervical vertebrae or of the metatarsals. Cluster d, on the other hand, consists of the three genera, Microdipodops, Dipodomys and Jaculus, in which saltatorial adaptations are most advanced. The hind legs and tail are greatly elongated and the forelegs reduced in proportion to the body. The bullae are inflated and the cervical vertebrae fused. In Jaculus, the metatarsals are fused and the first and fifth digits of the foot are lost. Clusters b and c contain forms which do not show saltatorial adaptations. Cluster c consists of the three genera Neotoma, Rattus and Heteromys whose members are the least specialised of the forms considered here.

2 Cluster analysis of distances between forms

The dendrogram produced by the cluster analysis of the distances between the 24 forms is shown in Fig. 5.2. A comparison of this dendrogram with that based on correlations shows that the diversity within and between species is not as clearly separated in the dendrogram based on distances as in that based on correlations and that the separation of the forms into species is not as good. One member of Rattus links with the members of Neotoma, two members of Dipodomys

Figure 5.2

Dendrogram produced by unweighted pair-group cluster analysis of distances between rodents. Distances based on standardised character values, The average distance between Pedetes (forms 39,40) and the other forms is 3.561.


54
55
56
Zapus
57
58
59
60
Napaeozapus
61
53
Sicista
13
16
15
Perognathus
14
21
23
24
Liomys
22
47
48
Gerbillus
17
20
18
Microdipodops
19
49
50
51
Tatera
52
64
Alactagulus
25
Heteromys
1
3
2
D. merriami
4
11
12
D. nitratoides
5
6
D. spectabilis
9
10
D. ordii
7
8
D. deserti
46
43
44
Neotoma
45
41
42
Rattus
62
63
Jaculus
26
27
28
Thomomys
29
30
31
32
Geomys
33
34
Orthogeomys
35
Zygogeomys
36
37
Cratogeomys
38
Heterogeomys
39
40
Pedetes
2.0
1.6
1.2
0.8
0.4
0.0

merriami link with the members of P. nitratoides and three members of Geomys link with the members of Thomomys.

The members of the Geomyidae and Zapodidae again form distinct clusters but the other genera do not fall into clusters which correspond to families nor is there any obvious grouping of genera which show similar functional adaptations. The distance coefficient is more sensitive to differences in size than the correlation coefficient and it is reasonable to conclude that the differences between the dendrograms are due to this greater sensitivity to size differences. The position of Pedetes in the two dendrograms supports this conclusion. The members of Pedetes are very much larger than the members of any of the other genera. An indication of the overall size of a form is provided by the length of its head and body. This length can be approximated by the sum of the values of characters 26,171,179 and 182 (see Table 5.2). The average value of these characters in Pedetes is 28.86cm. The genus with the next largest average value is Orthogeomys which has a value of 17.54cm. The remaining genera have values between 15.83cm and 4.47cm (see Table 5.3) The difference in size between Pedetes and the other genera corresponds to its extremely isolated position in the dendrogram based on distances. In the dendrogram based on correlations, on the other hand, Pedetes

has a more intermediate position.

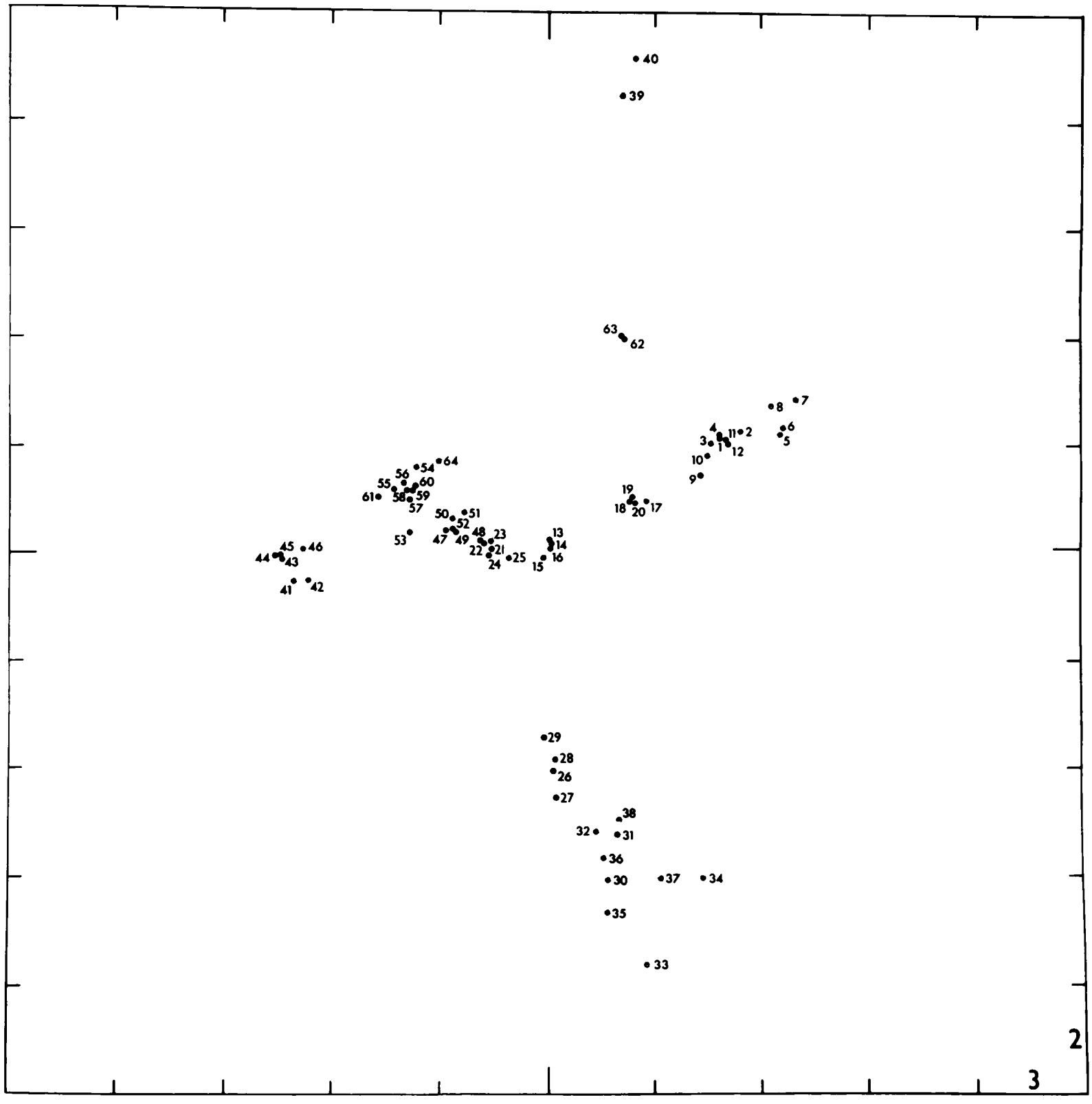
The comparisons between the dendrograms based on the two methods of measuring overall resemblance show clearly that the correlation coefficient gives a more informative picture of relationships than does the distance coefficient. The correlation coefficient gives a better separation of the forms into their species and gives a clearer picture of the "distinctiveness" of the species, that is, it shows more clearly the separation of within and between species diversity. Neither coefficient produces a pattern of relationships which shows complete agreement with the present taxonomic arrangement of the species but the clusters based on correlation coefficients are clusters of forms showing similar functional adaptations.

3 Principal components analysis of character covariances

The first three latent vectors of the table of covariances between characters were extracted by means of principal components analysis. The projections of the 64 forms onto each of these vectors were obtained in order to examine the distribution of the forms in the space defined by the first three vectors (see p.42). The positions of the 64 forms with respect to the second and third latent vectors are shown in Fig. 5.3. The positions of the 25 species with

Figure 5.3

Diagram to show the results of a principal components analysis of rodent character correlations. Forms plotted with respect to 2nd and 3rd latent vectors.


40
39
63
62
8
7
4
11
2
6
3
1
12
5
10
9
64
54
56
55
60
61
58
59
57
19
18
20
17
50
51
52
48
23
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24
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14
15
16
45
46
44
43
41
42
29
28
26
27
38
32
31
36
30
37
34
35
33
2
3

respect to the first three latent vectors are shown in Fig. 5.4. Each sphere in this model is at the centroid of the cluster of individuals representing a species. Pedetes is not shown in this model since its height above the base is more than twice that of species 12 (Orthogeomys) which is the highest species shown in the model. Its inclusion would have necessitated a reduction in the scale of the model which would have obscured the relationships of the other species. Its position with respect to these may be judged from Fig. 5.3.

The first three latent vectors account for 84.9% of the total variance of the characters and therefore the amount of distortion of relationships produced by projecting the forms into a space of only three dimensions is small. An examination of the model (Fig. 5.4) shows that a large proportion of the variation among the species is in the vertical dimension (i.e. is accounted for by the first latent vector). The height of a species above the base shows a close correspondence to its size when this is measured by the average length of head and body of the forms representing the species. These lengths are listed, in order of magnitude, in Table 5.3. It is reasonable to conclude, therefore, that the information provided by the first latent vector is mainly information

Figure 5.4 (a)

Model to show the results of the principal components analysis of rodent character correlations. The vertical axis corresponds to the 1st latent vector and the horizontal axes to the 2nd and 3rd latent vectors. Reference numbers on base as in Table 5.1.

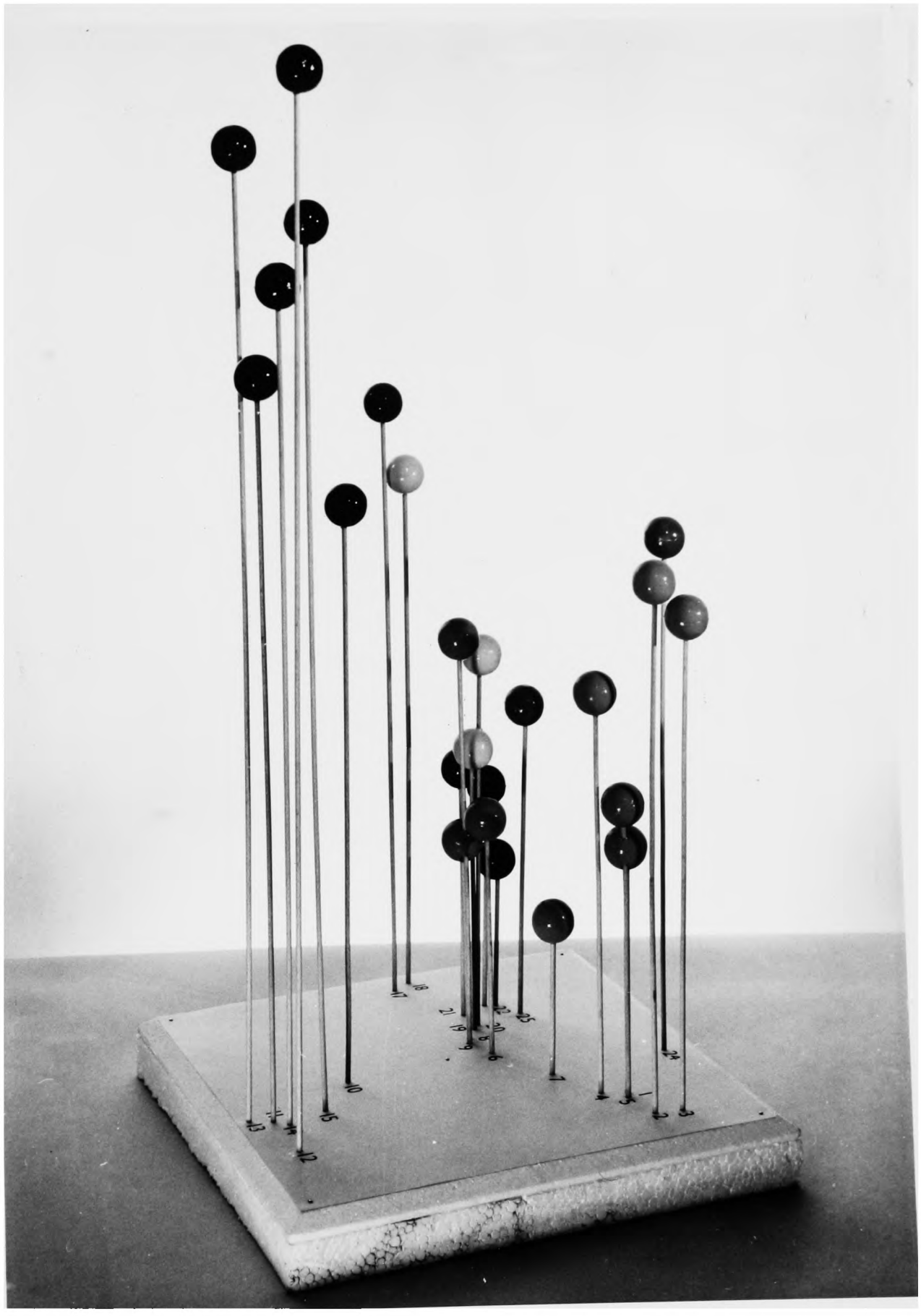
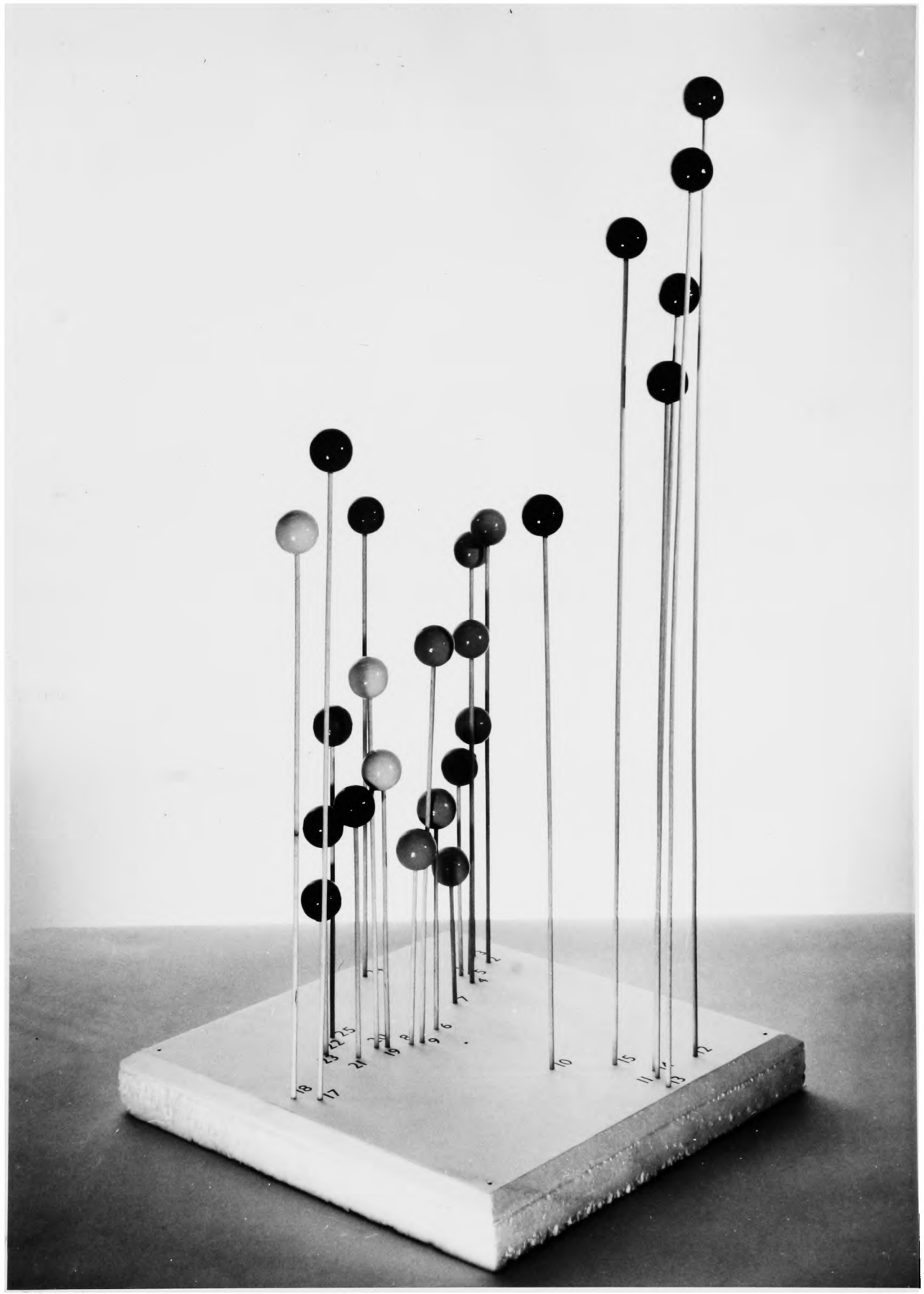


Figure 5.4 (b)

Model to show the results of the principal components analysis of rodent character correlations. The vertical axis corresponds to the 1st latent vector and the horizontal axes to the 2nd and 3rd latent vectors. Reference numbers on base as in Table 5.1.



about differences in size. It is possible, therefore, to ignore these differences in size by examining the distribution of the forms with respect to the second and third latent vectors only.

A comparison between the results of the principal components analysis and the results of the cluster analysis shows very clearly that the principal components analysis provides more information about the inter-relationships of the species since it shows each species in relation to all the others. The cluster analysis, on the other hand, only shows the way in which the species link together in clusters. For example, in the dendrogram based on correlations (Fig. 5.1), Perognathus and Liomys link with the Zapodidae - Tatera - Gerbillus group and Microdipodops with Dipodomys. Principal components analysis shows a similar pattern of relationships but also shows that Microdipodops (species 7) lies between the Dipodomys group (species 1 - 5) and the Perognathus - Liomys group (species 6,8).

In the results of the principal components analysis, the Geomyidae (species 10 - 15) are clearly separated from the rest of the species, as in the dendrograms produced by cluster analysis. The remaining species, with the exception of those of Pedetes and Jaculus (species 16, 24),

form a long narrow cluster with the unspecialised species of Rattus and Neotoma (species 17, 18) at one end and the highly saltatorial species of Microdipodops and Dipodomys (species 7 and 1 - 5) at the other. The remaining highly saltatorial species, those of Pedetes and Jaculus, also lie at considerable distances from Rattus and Neotoma but in different directions. Within the long narrow cluster, the species group together in a way which shows a fairly good agreement with that shown by cluster analysis. When the effects of differences in size are reduced, by projecting the forms onto the second and third vectors only (Fig. 5.3), the pattern of relationships produced is in fairly good agreement with that shown in the dendrogram based on the correlation coefficient, in which the effects of size differences are also reduced. There are, however, a number of differences in detail. Heteromys (form 25), for example, lies between Liomys and Perognathus (forms 13-16, 21-24) in the principal components diagram but close to Rattus and Neotoma (forms 41-46) in the dendrogram. The former position is more in agreement with the usual taxonomic position of Heteromys. Pedetes (forms 39, 40) also lies close to Rattus and Neotoma in the dendrogram but far from them in the principal components diagram, a position which reflects more accurately the differences in functional

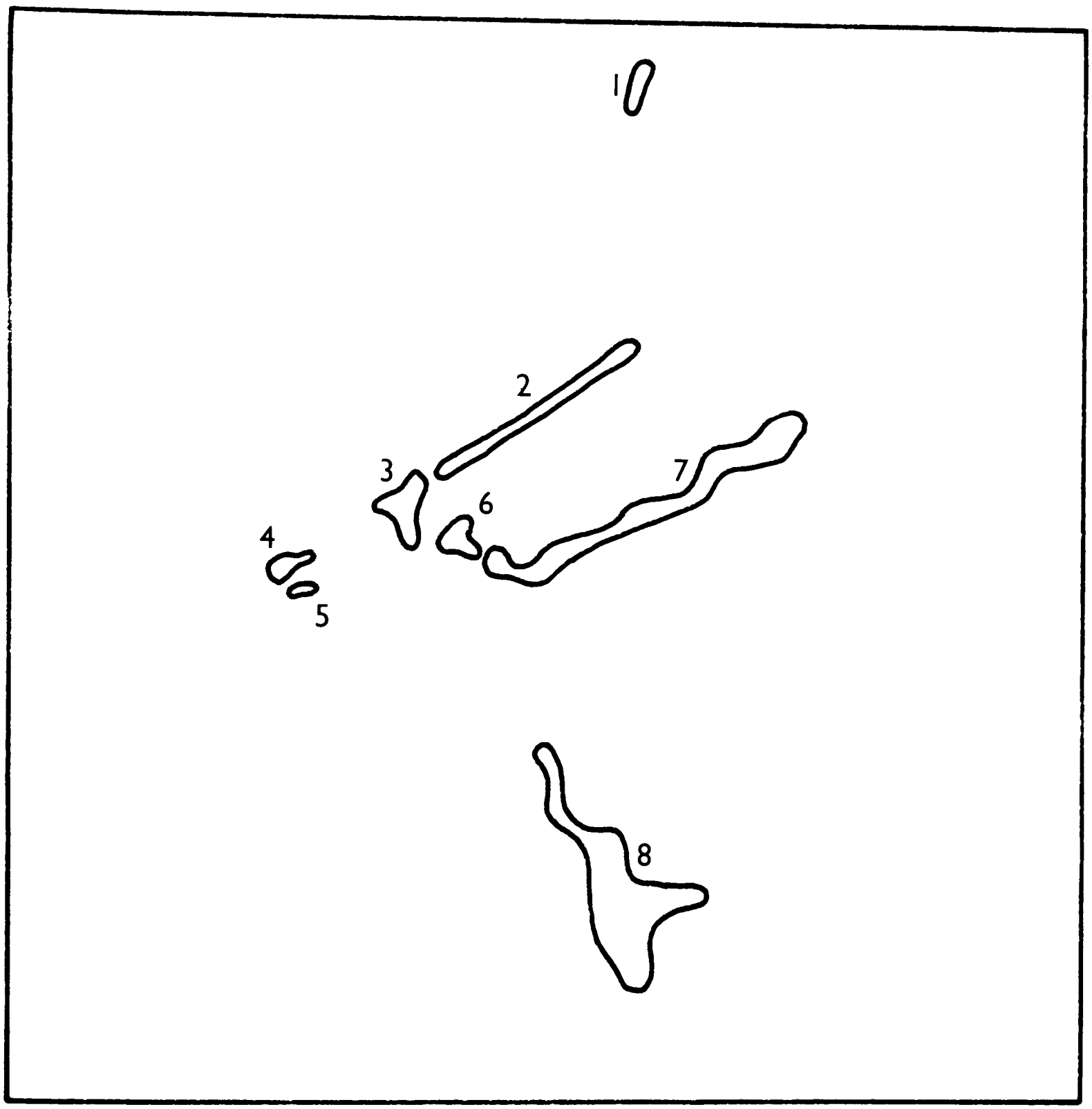
adaptation between its members and those of Rattus and Neotoma. The division of forms into species is not as clear in the principal components diagrams as in the dendrogram.

The approximate distribution in the space defined by the second and third vectors, of the seven families considered here is shown in Fig. 5.5. Since the large family, Cricetidae, is represented here by only three genera it is divided, for the purpose of the diagram, into 2 parts: Neotoma and the Gerbillinae, here represented by Gerbillus and Tatera. This diagram shows very clearly the different degrees of morphological diversity within each of the families. Although the family Dipodidae (2) is represented here by only two of its ten genera, it is clear that the range of diversity within it is much greater than that within the Zapodidae (3). The elongation of the clusters representing the families Dipodidae (2) and Heteromyidae (7) reflects the wide diversity of functional adaptation shown within these families. The similarities in functional adaptation between the saltatorial members of the two families are not sufficient to produce any overlap of the families. The wide divergence in functional adaptation between the Heteromyidae (7) and the Geomyidae (8) is clearly shown. It is clear, however, from a comparison of Fig. 5.3 with Fig.5.5, that the major gaps

Figure 5.5

Diagram to show the approximate distribution in the space defined by the 2nd and 3rd latent vectors of the taxonomic groups considered in this study.

1 = Pedetidae, 2 = Dipodidae, 3 = Zapodidae,
4 = Leotoma, 5 = Rattus, 6 = Gerbillinae,
7 = Heteromyidae, 8 = Geomyidae.


1
2
3
4
5
6
7
8

between the forms, in the space defined by the second and third vectors, do not always correspond to the divisions between the families. Some of the gaps between genera within the Heteromyidae (forms 1-25), for example, are considerably larger than the gap between the Heteromyidae and the Gerbillinae (forms 47-52).

The results of the principal components analysis of covariances between characters suggest that this is a useful method of investigating the diversity of forms. The pattern of relationships that it produces is similar to that produced by a cluster analysis of the similarities between the forms but it provides more information about the inter-relationships of forms.

5.4 Summary

The following conclusions can be drawn from the results of the analyses reported in this chapter.

1. The correlation coefficient produces a more informative picture of the relationships between forms than does the distance coefficient. Neither coefficient produces a pattern of relationships in complete agreement with the existing taxonomic arrangement of the forms considered. The relationships shown by the correlation coefficient correspond to similarities and differences

in functional adaptation whereas those shown by the distance coefficient correspond more to similarities and differences in overall size.

2. The pattern of relationships produced by a principal components analysis of covariances between characters contains information about resemblances in size and shape. The effects of size may be reduced by ignoring the first latent vector of the table of covariances. The pattern of relationships with respect to the second and third latent vectors is in fairly good agreement with that produced by a cluster analysis of correlations between the forms. It gives a clearer picture of the inter-relationships of the forms than does the cluster analysis.

3. The distribution of the families in the space defined by the second and third latent vectors clearly shows the differences in diversity within and between the families. Similarities between the members of different families adapted to a jumping mode of progression are not sufficient to produce any overlap of the families in this space.

4. Although the study reported in this chapter is only exploratory, its results do provide further confirmation of the usefulness of quantitative methods in analysing taxonomic relationships.

TABLE 5.1

LIST OF RODENT SKELETONS MEASURED

HETEROMYIDAE	Dipodomys merriami (1)	1 - 4
	Dipodomys spectabilis (2)	5 - 6
	Dipodomys deserti (3)	7 - 8
	Dipodomys ordii (4)	9 - 10
	Dipodomys nitratoides (5)	11 - 12
	Perognathus hispidus (6)	13 - 16
	Microdipodops pallidus (7)	17 - 20
	Liomys salvini (8)	21 - 24
	Heteromys desmarestianus (9)	25
GEOMYIDAE	Thomomys umbrinus (10)	26 - 29
	Geomys bursarius (11)	30 - 33
	Orthogeomys grandis (12)	34
	Zygogeomys trichopus (13)	35
	Cratogeomys castanops (14)	36 - 37
	Heterogeomys hispidus (15)	38
PEDETIDAE	Pedetes cafer (16)	39 - 40
MURIDAE	Rattus norvegicus (17)	41 - 42
CRICETIDAE	Neotoma albigula (18)	43 - 46
	Gerbillus campestris (19)	47 - 48
	Tatera lobengulae (20)	49 - 52

Each skeleton was given a reference number and these numbers appear in the right-hand column. Reference numbers used in Fig. 5.4 are shown in brackets.

TABLE 5.1-- Continued

ZAPODIDAE	Sicista betulina (22)	53
	Zapus princeps (21)	54 - 57
	Napaeozapus insignis (23)	58 - 61
DIPODIDAE	Jaculus orientalis (24)	62 - 63
	Alactagulus pumilio (25)	64

TABLE 5.2

LIST OF RODENT CHARACTERS

BRAIN CASE, BASE OF SKULL, ARTICULAR REGION

1 Distance in the median sagittal plane from the anterior margin of the basioccipital to the anterior margin of the foramen magnum.

2 Distance between the most lateral points on the lateral borders of the condyles.

3 Distance between the lateral apices of the exoccipital processes.

4 Distance from the lateral apex of the exoccipital process to the anterior margin of the basioccipital, in the median sagittal plane.

5 Distance from the basioccipital-basisphenoid suture, (or posterior end of the junction of the cornua), to the posterior point on the margin of the palatine between the roots of the hamular processes, in the median sagittal plane. Ignore palatal spine if present.

6 Maximum length of the middle lacerated foramen, (between the alisphenoid and the audital bulla). Measure only when distinct foramen is present.

7 Greatest length of the posterior lacerated foramen (between the basioccipital and the audital bulla; there may be several, if so, length between the most distant).

8 Distance between the anterior ends of the middle and posterior lacerated foramina. Use points defined in 6 and 7.

9 Length, in the median sagittal plane, of the foramen magnum.

10 Greatest breadth of the foramen magnum, normal to the length.

11 Length of the suture between the supraoccipital and the parietals and interparietal(s).

12 Length of the suture between the supraoccipital and the inter-parietal(s).

13 Length of the posterior border of the parietal(s). The lateral reference points are the posterior ends of the squamosal-parietal sutures.

14 Length of the parietal-interparietal suture.

TABLE 5.2- Continued

15	Width of the interparietal(s).
16	Length, measured as a direct line, of the edge of the parietal between the posterior end of the squamosal-parietal suture and the parietal-frontal-squamosal junction.
17	Distance in the median sagittal plane between the anterior and posterior borders of the interparietal(s).
18	Distance between two points, each defined by the posterior end of the dorsal suture between the maxilla and the premaxilla.
19	Distance between two points, each defined by the postero-lateral end of the dorsal suture between the maxilla and the frontal.
20	Maximum distance between the most lateral points on the borders of the lachrymals.
21	Distance, in a direct line, between the ends of the maxilla-frontal suture.
22	Distance between two points, each defined by the frontal-parietal-squamosal junction.
23	Presence of an interfrontal suture.
24	Distance in the median sagittal plane, from the posterior margin of the interparietal(s) to the anterior tip of the nasals.
25	Distance from the most anterior point on the anterior margin of the foramen magnum to the midpoint of a line tangent to the posterior borders of the incisor alveoli.
26	Distance from the most posterior point on the posterior margin of the foramen magnum to the midpoint of a line tangent to the posterior borders of the incisor alveoli.
27	Distance in the vertical plane from the most posterior point on the posterior margin of the foramen magnum to the most posterior point on the posterior margin of the interparietal(s).

MASTICATORY COMPLEX

28	Distance between the most lateral points on the lateral margins of the incisor alveoli.

29 Presence of grooving on the incisors.

30 Distance between the midpoints of lines tangent to the anterior and posterior borders of the incisor foramina.

31 Maximum distance between the lateral borders of the incisor foramina.

32 Length of the upper diastema from the midpoint of a line tangent to the posterior margins of the incisor alveoli to the midpoint of a line tangent to the anterior margins of the premolar alveoli, (or first molar if premolars are absent).

33 Length of the tooth row from the anterior margin of the premolar or first molar alveolus to the posterior margin of the third molar alveolus.

34 Greatest length, parallel to the tooth plane, of the infra-orbital foramen.

35 Width of the infra-orbital foramen, normal to the greatest length.

36 Distance from the most posterior point on the posterior margin of the infra-orbital foramen to the midpoint of the maxilla-palatine suture.

37 Distance between the most anterior points on the anterior margins of the infra-orbital foramina.

38 Distance between the most posterior points on the posterior margins of the infra-orbital foramina.

39 Length of the infra-orbital fenestration from the most ventral point on the ventral border to the most posterior point on the dorsal border.

40 Distance along a horizontal line between the points defined in 39.

41 Distance from the ventral point defined in 39 to the most anterior point on the curve of the maxillar root of the zygoma.

42 Width between the most lateral points on the lateral borders of the fenestration.

43 Distance from the most posterior point on the dorsal border of the fenestration to the most posterior point on the curve of the maxillar root of the zygoma.

44 From the most posterior point on the dorsal border of the fenestration to the lateral point defined in 42.

TABLE 5.2- Continued

45	Distance in the median sagittal plane from the premaxilla-maxilla suture to the maxilla-palatine suture.
46	Distance in the median sagittal plane from the maxilla-palatine suture to the posterior border of the palatine (not including the median palatal spine).
47	Distance across the palate between the medial margins of the premolar alveoli.
48	Distance across the palate between the medial margins of the first molar alveoli.
49	Distance across the palate between the medial margins of the third molar alveoli.
50	Distance from the midpoint of the maxilla-palatine suture to the midpoint of a line joining the lateral portions of the maxilla-palatine suture.
51	Length of the boundary of the insertion of the masseter, from the maxillary to the squamosal root of the zygoma.
52	Length of the vertical component of the jugal, from its dorsal apex to the midpoint of the junction between the anterior and ventral borders.
53	Length of the horizontal component of the jugal, from the midpoint of the junction between the anterior and the ventral borders to its posterior end.
54	Minimum width of the horizontal component of the jugal, measured parallel to the tooth plane.
55	Dorsoventral length of the squamosal from the posterior end of the squamosal-jugal junction to the squamosal-parietal-frontal junction.
56	Length, in a direct line, of the mastoid projection of the squamosal, from its origin on the posterior border of the squamosal to its posterior apex.
57	From the most ventral point on the ventral border of the squamosal to a point on the dorsal border vertically above.
58	Length of the squamosal from the posterior end of the parietal- squamosal suture to the squamosal-frontal-alisphenoid junction, if alisphenoid is present; to the anterior end of the squamosal-frontal suture if the alisphenoid is absent.

59	Length of the glenoid fossa along the major axis of the groove.
60	Breadth of the glenoid fossa, normal to the length.
61	Distance between the midpoints of the squamosal roots of the zygomatic bars.
62	Maximum distance between the lateral surfaces of the jugals.
63	Distance between the lateral apices (standing free of the zygoma) of the maxillary flanges of the zygomatic bars.
64	Length of the zygomatic bar from the midpoint of the squamosal root to the most anterior point on the posterior curve of the maxillar portion of the zygoma.
65	Maximum length, along the major axis of the tooth row, of the surface of the crown of the premolar.
66	Breadth, normal to the maximum length, of the surface of the crown of the premolar.
67	Maximum length, along the major axis of the tooth row, of the surface of the crown of the first molar.
68	Breadth, normal to the maximum length, of the surface of the crown of the first molar.
69	Maximum length, along the major axis of the tooth row, of the surface of the crown of the second molar.
70	Breadth, normal to the maximum length, of the surface of the crown of the second molar.
71	Maximum length, along the major axis of the tooth row, of the surface of the crown of the third molar.
72	Breadth, normal to the maximum length, of the surface of the crown of the third molar.

MANDIBLE

73	Distance between the centres of the articular surfaces.
74	Greatest length of the articular surface.
75	Distance from the midpoint of a line tangent to the posterior borders of the incisor alveoli to the centre of the articular surface.

TABLE 5.2- Continued

76	Presence of a fenestration at the base of the articular process.
77	Distance between the apices of the coronoid processes.
78	Presence of a fenestration at the base of the coronoid process.
79	Distance between the lateral apices of the angular processes.
80	Distance between two points each defined by the junction of the medial and posterior borders of the angular processes.
81	Length of the posterior border of the angular process.
82	Distance from the centre of the articular surface to the ventral junction (defined in 80) of the borders of the angular processes.
83	Distance from the apex of the coronoid process to the ventral junction of the borders of the angular process.
84	Distance between the most medial points on the medial margins of the premolar alveoli.
85	Distance between the most medial points on the medial margins of the first molar alveoli.
86	Distance between the most medial points on the medial margins of the third molar alveoli.
87	Distance from the midpoint of a line tangent to the posterior borders of the incisor alveoli to the midpoint of a line tangent to the anterior borders of the premolar alveoli.
88	Length of the cheek teeth row from the anterior margin of the premolar alveolus to the posterior margin of the third molar alveolus.
89	Maximum length, along the major axis of the tooth row, of the surface of the crown of the premolar.
90	Breadth, normal to the maximum length, of the surface of the crown of the premolar.
91	Maximum length, along the major axis of the tooth row, of the surface of the crown of the first molar.
92	Breadth, normal to the maximum length, of the surface of the crown of the first molar.

93 Maximum length, along the major axis of the tooth row, of the surface of the crown of the second molar.

94 Breadth, normal to the maximum length, of the surface of the crown of the second molar.

95 Maximum length, along the major axis of the tooth row, of the surface of the crown of the third molar.

96 Breadth, normal to the maximum length, of the surface of the crown of the third molar.

97 Distance between the most lateral points on the lateral margins of the incisor alveoli.

98 Length of the incisor, measured to the tip, from the anterior margin of the alveolus.

SENSORY REGIONS

99 Distance from the parietal-frontal-squamosal junction to the ventral base of the lateral maxilla-palatine suture.

100 Distance from the squamosal root of the zygomatic bar to the lachrymal-frontal-maxilla junction.

101 Maximum length of the inner diameter of the external audital meatus, parallel to the tooth plane.

102 Maximum width of the inner diameter of the external audital meatus, normal to the maximum length.

103 Length of the tubular projection of the external audital meatus, measured on the ventral surface to its root on the audital bulla.

104 Distance from the most posterior point on the posterior margin of the external audital meatus to the midpoint of the posterior border of the interparietal(s).

105 Distance from the point defined in 104 to the midpoint of the anterior margin of the foramen magnum.

106 Distance from the point defined in 104 to the narrowest width of the supraoccipitals.

107 Distance from the point defined in 104 to the squamosal-frontal-alisphenoid junction, (if alisphenoid is absent, measure to the anterior end of the frontal-alisphenoid suture).

TABLE 5.2- Continued

108	Distance between the dorsal apices of the mastoid bullae.
109	Distance between the most posterior points on the posterior margins of the external audital meati.
110	Minimum distance between the borders of the supraoccipitals and the mastoid bullae.
111	Distance between the ventral apices of the cornua of the audital bullae.
112	Length of the junction between the ventral apices of the cornua of the audital bullae.
113	Greatest length of the ventral surface of the audital bulla.
114	Breadth of the nasal cavity.
115	Length, in the median sagittal plane, of the nasal cavity.

PTERYGOID COMPLEX

116	Greatest distance between the lateral borders of the lateral plates of the parapterygoid fossae.
117	Least distance between the lateral borders of the lateral plates of the mesapterygoid fossae.
118	Distance from the anterior borders of the mesapterygoid fossa to the posterior border of the basisphenoid in the median sagittal plane.
119	Length of the medial palatal spine.
120	Length of the external plate of the mesapterygoid fossa (this is the Hamular process).
121	Distance between the posterior tips of the Hamular processes.
122	Minimum distance between the external plates of the mesapterygoid fossae.

PECTORAL GIRDLE

123	Width of the supraspinous fossa, normal to the axis of the spine, measured from the spine to a line tangent to the anterior border and parallel to the axis of the spine.

TABLE 5.2- Continued

124	Maximum width of the infraspinous fossa, normal to the axis of the spine, measured from the spine (or its extension) to a line tangent to the axillary border and parallel to the axis of the spine.
125	Length of the anterior border, from the edge of the glenoid cavity, ignoring any coracoid process, to the centre of the angle with the vertebral border.
126	Length of the axillary border, from the edge of the glenoid cavity to the centre of the angle with the vertebral border.
127	Length of the vertebral border, between its junctions with the anterior and axillary borders.
128	Maximum length of the spine of the scapula, from its origin on the scapular plate to the tip of the acromion process.
129	Length along the axis of the spine from the vertebral edge to the edge of the glenoid cavity.
130	Maximum width across the acromion and metacromion, measured normal to the axis of the spine.
131	Length of the junction between the spine and the scapular plate.
132	Maximum vertical height of the spine, normal to the scapular plate.
133	Length of the extension of the edge of the glenoid cavity (coracoid process), measured along an axis parallel to the axis of the spine, from the main edge to the apex of the extension.
134	Maximum length of the clavicle, measured as a straight line between its tips.

FORE-LIMB

135	Distance from the centre of the head to the centre of the distal articular surface between the condyles.
136	Distance from the center of the head to the apex of the deltoid tuberosity.
137	Length of the base of the supinator crest.
138	Minimum width of the shaft.

TABLE 5.2- Continued

139	Distance across the tubercles, from the apex of the greater to the apex of the lesser tubercle.
140	Distance between the most lateral points on the lateral surfaces of the epicondyles.
141	Presence of an entepicondylar foramen.
142	Width across the distal articular surface.
143	Length of the radius from its proximal face (the distal wall of the semilunar notch) to its distal apex.
144	Length of the ulna from the base of the semilunar notch to its distal apex.
145	Distance from the base of the semilunar notch to the proximal apex of the olecranon.
146	Minimum width of the shaft of the ulna, with the floor of the semilunar notch in a horizontal plane.
147	Minimum width of the shaft of the radius, with the floor of the semilunar notch in a horizontal plane.
148	Number of digits.
149	Length of the 1st metacarpal.
150	Length of the 1st phalanx of the 1st digit.
151	Length of the 2nd phalanx of the 1st digit.
152	Length of the 3rd phalanx of the 1st digit.
153	Length of the 2nd metacarpal.
154	Length of the 1st phalanx of the 2nd digit.
155	Length of the 2nd phalanx of the 2nd digit.
156	Length of the 3rd phalanx of the 2nd digit.
157	Length of the 3rd metacarpal.
158	Length of the 1st phalanx of the 3rd digit.
159	Length of the 2nd phalanx of the 3rd digit.
160	Length of the 3rd phalanx of the 3rd digit.
161	Length of the 4th metacarpal.
162	Length of the 1st phalanx of the 4th digit.
163	Length of the 2nd phalanx of the 4th digit.

TABLE 5.2- Continued

164	Length of the 3rd phalanx of the 4th digit.
165	Length of the 5th metacarpal.
166	Length of the 1st phalanx of the 5th digit.
167	Length of the 2nd phalanx of the 5th digit.
168	Length of the 3rd phalanx of the 5th digit.

VERTEBRAL COLUMN

169	Number of cervical vertebrae.
170	Number of fused units among the cervical vertebrae, (Hatt).
171	Length of the cervical region, between the articular surfaces, measured along the ventral surface.
172	Maximum width of the atlas.
173	Maximum height of the atlas, normal to the maximum length.
174	Maximum width of the axis, measured across the articular surfaces.
175	Height of the axis, measured to the inner roof of the neural arch, normal to the maximum width.
176	Length of the base of the axis, measured along the mid line.
177	Height of the spine of the axis, measured from the inner roof of the neural arch to the apex of the spine.
178	Number of thoracic vertebrae.
179	Length of the thoracic region, measured between the articular surfaces, along the ventral surface.
180	Length of the sternum.
181	Number of lumber vertebrae.
182	Length of the lumbar region, measured between the articular surfaces, along the ventral surface.
183	Average number of sacral vertebrae, (Hatt).
184	Average number of pseudosacral vertebrae, (Hatt).

185 Proportionate length of the sacrum-pseudosacrum.

186 Length of the caudal region,

187 Number of caudal vertebrae (Hatt).

PELVIC GIRDLE

188 Length of the pubic symphysis.

189 Distance from the centre of the acetabulum to the apex of the superior ischial tuberosity.

190 Distance from the centre of the acetabulum to the base of the gluteal notch.

191 Distance from the bottom of the gluteal notch to the apex of the iliac crest.

192 Distance from the centre of the acetabulum to the apex of the femoral process.

193 Distance from the apex of the femoral process to the apex of the iliac crest.

194 Distance from the apex of the superior ischial tuberosity to the posterior end of the pubic symphysis.

195 Distance from the anterior end of the pubic symphysis to the apex of the ilio-pectineal eminence (first not second projection).

196 Distance from the apex of the femoral process to the superior ventral spine.

197 Distance from the dorsal to the ventral spine via the crest and apex of the ilium.

198 Maximum length of the obdurator foramen.

199 Maximum width of the obdurator foramen, normal to the maximum length.

200 Distance between the apices of the ischial tuberosities.

201 Distance between the bases of the gluteal notches.

202 Distance between the apices of the iliac crests.

203 Maximum inner diameter of the acetabulum.

204 Maximum width, normal to the midline, of the superior gluteal fossa

TABLE 5.2- Continued

205	Maximum width, normal to the midline, of the inferior gluteal fossa.
206	Distance from the centre of the acetabulum to the most ventral point on the anterior articular surface of the first sacral vertebra.
HIND-LIMB	
207	Distance from the fovea of the head to the centre of the face of the greater trochanter.
208	Distance from the fovea to the apex of the lesser trochanter.
209	Distance from the fovea to the apex of the 3rd trochanter.
210	Distance from the centre of the face of the greater trochanter to the most distal point between the condyles.
211	Distance from the fovea to the most distal point between the condyles.
212	Maximum width across the condyles.
213	Minimum width of shaft.
214	Length of the tibia from the centre of the proximal articular surface to the centre of the distal articular surface.
215	Minimum width of the shaft.
216	Length of the free portion of the fibula.
217	Length of the crest.
218	Over-all length of the calcaneum.
219	Minimum width of the calcaneum.
220	Length of the astragulus measured from the centre of its articulation with the tibia to its distal end.
221	Distance from the anterior end of the astragulus to the centre of its articulation with the calcaneum.
222	Width of the astragulus measured across its articulation with the tibia.

TABLE 5.2 - Continued

223	Distance from the posterior end of the calcaneum to the centre of its articulation with the astragalus.
224	Number of digits.
225	Length of the 1st metatarsal.
226	Length of the 1st phalanx of the 1st digit.
227	Length of the 2nd phalanx of the 1st digit.
228	Length of the 3rd phalanx of the 1st digit.
229	Length of the 2nd metatarsal.
230	Length of the 1st phalanx of the 2nd digit.
231	Length of the 2nd phalanx of the 2nd digit.
232	Length of the 3rd phalanx of the 2nd digit.
233	Length of the 3rd metatarsal.
234	Length of the 1st phalanx of the 3rd digit.
235	Length of the 2nd phalanx of the 3rd digit.
236	Length of the 3rd phalanx of the 3rd digit.
237	Length of the 4th metatarsal.
238	Length of the 1st phalanx of the 4th digit.
239	Length of the 2nd phalanx of the 4th digit.
240	Length of the 3rd phalanx of the 4th digit.
241	Length of the 5th metatarsal.
242	Length of the 1st phalanx of the 5th digit.
243	Length of the 2nd phalanx of the 5th digit.
244	Length of the 3rd phalanx of the 5th digit.

TABLE 5.3

OVERALL LENGTHS (EXCLUDING TAIL) OF SKULLS*

1	**Pedetes** (16)	28.86 cm
2	**Orthogeomys** (12)	17.54
3	Lycogeomys (13)	15.83
4	**Heterogeomys** (15)	15.13
5	**Rattus** (17)	14.37
6	**Cratogeomys** (14)	13.64
7	**Geomys** (11)	13.23
8	Thomomys (10)	12.8[illegible]
9	Neotoma (18)	12.4[illegible]
10	**Heteromys** (9)	9.43
11	**Jaculus** (24)	9.35
12	**Tatera** (20)	8.85
13	**Dipodomys** deserti (3)	8.43
14	**Dipodomys** ordii (4)	7.77
15	Dipodomys spectabilis (2)	7.7[illegible]
16	**Gerbillus** (19)	7.32
17	**Alactagulus** (25)	6.94
18	**Zapus** (21)	6.9[illegible]
19	**Dipodomys** merriami (1)	6.46
20	**Perognathus** (6)	6.40
21	Dipodomys **nitratoides** (5)	6.31
22	Liomys (8)	6.22
23	Napaeozapus (23)	6.[illegible]1
24	**Sicista** (22)	5.[illegible]3
25	Microdipodops (7)	4.47

* Sum of mean values for individual within each group, of characters 26, 171, 179, 182 (see Table 5.2).

6 CONCLUSIONS

The purpose of this thesis has been to compare the relative merits of several quantitative methods of analysing taxonomic relationships and to examine the kinds of information these provide. A detailed summary of the thesis is not given here since each chapter of the thesis has its own summary. The purpose of this final chapter is to present, briefly, the main conclusions of the thesis.

1. The purpose of a phenetic classification is to provide a map of the diversity of organisms which is as objective and informative as possible. The studies reported in this thesis show clearly that quantitative methods can play an important part in the construction of such a classification. The advantages of quantitative methods over other methods of constructing classifications are: firstly, they ensure that all characters of organisms are explicitly taken into account; secondly, they ensure that the information provided by different characters is not weighted according to pre-conceived ideas as to the relative importance of these characters; thirdly, they permit degrees of relationship to be expressed in precise rather than vague terms; fourthly, they provide a means of expressing the multi-dimensional relationships of organisms in an easily-understood way

2. A phenetic classification is based on the overall resemblances of organisms. Five coefficients of similarity were considered in this thesis. Each is a valid measure of overall resemblance. It is possible to separate the contribution to overall resemblance of morphological characters into size and shape components. The five coefficients differ in the relative emphasis they give to these components. By a suitable choice of similarity coefficient, therefore, the taxonomist can see to what extent the morphological resemblance between organisms is due to similarities in shape and how much to similarities in size. A classification based on resemblances in which there is a large size component is likely to be less informative than one based on resemblance from which the size component has been removed. Of the five coefficients, the correlation coefficient is least sensitive to the size component of resemblance.

3. Two kinds of methods of analysing tables of similarity values were considered in the thesis, cluster analysis and principal components analysis. The relative merits of these may be judged either by the faithfulness with which they reproduce a table of similarity values or by the way in which they represent relationships. Cluster analysis is more useful than principal components analysis if the

purpose is to construct a classification which takes the form of a hierarchy of discrete classes. However, principal components analysis provides more information about the inter-relationships of organisms. It is an effective method of constructing a quantitative map in two or three dimensions of the diversity of organisms.

4. The comparisons between the methods were based entirely on morphological characters. The patterns of relationship shown by the different methods are in fairly good agreement with those based on intuitive assessments of morphological resemblance. They show less agreement, however, with relationships based on non-morphological characters. It is difficult to say to what extent it is meaningful to base measures of overall resemblance on different kinds of characters. It would seem preferable to use a form of Adanson's own method, and to construct separate classifications on the basis of different kinds of characters and then to combine these to produce a single classification.

REFERENCES

BHATTACHARYYA, A. 1946. On a measure of divergence of two multinomial populations. Sankhya, 7: 401-406.

BIGELOW, R.S. 1956. Monophyletic classification and evolution. Systematic Zool., 5: 145-146.

BLACKITH, R.E. 1965. Morphometrics. In: T.H. Waterman and H.J.Morowitz (eds.), Theoretical and mathematical biology, pp.225-249. Blaisdell Publishing Company, New York. 426pp.

CAIN, A.J. 1954. Animal species and their evolution. Hutchinson, London.190pp.

——— 1958. Logic and memory in Linnaeus's system of taxonomy. Proc.Linn.Soc.Lond., 169th session, pp.144-163.

——— 1959a. Deductive and inductive methods in post-Linnaean taxonomy. Proc.Linn.Soc.Lond., 170th session, pp185-217.

——— 1959b. The post-Linnaean development of taxonomy. Proc. Linn.Soc.Lond., 170th session, pp.234-244.

CAIN, A.J. and HARRISON, G.A. 1958. An analysis of the taxonomist's judgment of affinity. Proc.Zool.Soc.Lond., 131: 85-98.

CAIN, A.J. and HARRISON, G.A. 1960. Phyletic weighting. Proc. Zool.Soc.Lond., 135: 1-31.

CAMPBELL, B.G. 1963. Quantitative taxonomy and human evolution. In: S.L.Washburn (ed.), Classification and human evolution, pp.50-74. Aldine Publishing Company, Chicago. 371pp.

CLARK, W.E.Le Gros. 1955. The fossil evidence for human evolution. The University of Chicago Press, Chicago. 101pp.

——— 1959. The Antecedents of Man. Edinburgh University Press, Edinburgh. 374pp.

COHEN, M.R. and NAGEL, E. 1934. An introduction to logic and scientific method. Routledge and Kegan Paul, London 467pp.

CZEKANOWSKI, J. 1932. "Coefficient of racial likeness" und "durchschnittliche Differenz". Anthrop.Anz., 9: 227-249.

DARWIN, C. 1891. The origin of species by means of natural selection. 6th ed. Murray, London. 432pp.

DAY, M.H. 1965. Guide to fossil man. A handbook of human palaeontology. Cassel, London. 289pp.

EDWARDS, A.W.F. and CAVALLI-SFORZA, L.L. 1964. Reconstruction of evolutionary trees. In: V.H.Heywood and J.McNeill (eds.), Phenetic and phylogenetic classification, pp.67-76. Systematics Association Publication No. 6, London.164pp.

——— 1965. A method for cluster analysis. Biometrics, 21: 362-375.

GILMOUR, J.S.L. and WALTERS, S.M. 1964. Philosophy and classification. In: W.B.Turrill (ed.), Vistas in Botany, Vol. 4, pp.1-22. Pergamon Press, Oxford. 314pp.

GOODMAN, M. 1963. Man's place in the phylogeny of the Primates as reflected in serum proteins. In: S.L.Washburn (ed.), Classification and human evolution, pp.204-234. Aldine Publishing Company, Chicago. 371pp.

GOWER, J.C. 1965. Some distance properties of latent root and vector methods used in multivariate analysis. (In press).

HARRISON, G.A. and WEINER, J.S. 1963. Some considerations in the formulation of theories of human phylogeny. In: S.L.Washburn (ed.), Classification and human evolution, pp. 75–84. Aldine Publishing Company, Chicago. 371pp.

HATT, R.T. 1932. The vertebral columns of ricochetal rodents. Bull.Am.Mus.Nat.Hist., 63: 599–738.

HEINCKE, F. 1898. Naturgeschichte des Herings. I. Die Lokalformen und die Wanderungen des Herings in den europaischen Meeren, Abh.Deutsch.Seefischerei-Vereins, 2: i–cxxxvi, 1–123.

HESLOP-HARRISON, J. 1962. Purposes and procedures in the taxonomic treatment of higher organisms. In: G.C.Ainsworth and P.H.A.Sneath (eds.), Microbial classification, 12th Symposium of the Society for General Microbiology, pp.14–36. Cambridge University Press, Cambridge. 483pp.

HOWELL, A.B. 1944. Speed in animals, their specialization for running and leaping. University of Chicago Press, Chicago. 270pp.

HUIZINGA, J. 1962. From DD to D^k and back. The quantitative expression of resemblance. Proc.K.ned.Akad.Wet.,Series C, 65: 380–391.

——— 1965. Some more remarks on the quantitative expression of resemblance (distance coefficients) Proc.K.ned.Akad.Wet., Series C, 68: 69–80.

KRUSKAL, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika, 29: 1–27.

MACNAUGHTON-SMITH, P., WILLIAMS, W.T., DALE, M.B. and MOCKETT, L.G. 1964. Dissimilarity analysis: a new technique of hierarchical sub-division. Nature, 202: 1034-1035.

MAHALANOBIS, P.C. 1930. On tests and measures of group divergence. Jour.Asiat.Soc.Bengal, 26: 541-588.

——— 1936. On the generalised distance in statistics. Proc.Nat. Inst.Sci.India, 2: 49-55.

MILLOT, F.C. 1965. The effects on classification of slight alterations in numerical techniques. Systematic Zool., 14: 196-213.

OLSON, E.C. and MILLER, R.L. 1958. Morphological integration. University of Chicago Press, Chicago. 317pp.

ORNSTEIN, L. 1965. Computer learning and the scientific method: a proposed solution to the information theoretical problem of meaning. J.Mount Sinai Hospital, 32: 437-494.

PENROSE, L.S. 1954. Distance, size and shape. Ann.Eugenics, 18: 337-343.

RAO, C.R. 1948. The utilisation of multiple measurements in problems of biological classification. Jour.Roy.Statist. Soc., 10: 159-193.

——— 1952. Advanced statistical methods in biometric research. John Wiley and Sons, New York. 319pp.

——— 1954. On the use and interpretation of distance functions in statistics. Bull.Int.Stat.Inst., 34: 3-10.

——— 1964. The use and interpretation of principal components analysis in applied research. Sankhya, 26: 329-358.

REYMENT, R.A. 1962. Observations on homogeneity of covariance matrices in paleontologic biometry. Biometrics, 18: 1-11.

ROHLF, F.J. and SOKAL, R.R. 1965. Coefficients of correlation and distance in numerical taxonomy. Univ.Kansas Sci.Bull., 45: 3-27.

SCHULTZ, A.H. 1963. Age changes, sex differences, and variability as factors in the classification of Primates. In: S.L.Washburn (ed.), Classification and human evolution, pp. 85-115. Aldine Publishing Company, Chicago. 371pp.

SIMPSON, G.G. 1945. The principles of classification and a classification of mammals. Bull.Am.Mus.Nat.Hist., 85: 1-350.

——— 1961. Principles of animal taxonomy. Columbia University Press, New York. 247pp.

SNEATH, P.H.A. 1957. Some thoughts on bacterial classification. J.Gen.Microbiol., 17: 184-200.

SOKAL, R.R. 1958. Quantification of systematic relationships and of phylogenetic trends. Proc.X Intern.Cong.Entomol., 1: 409-415.

——— 1961. Distance as a measure of taxonomic similarity. Systematic Zool., 10: 70-79.

SOKAL, R.R. and MICHENER, C.D. 1958. A statistical method for evaluating systematic relationships. Univ.Kansas Sci.Bull., 38: 1409-1438.

SOKAL, R.R. and ROHLF, F.J. 1962. The comparison of dendrograms by objective methods. Taxon., 11: 33-40.

SOKAL, R.R. and SNEATH, P.H.A. 1963. Principles of numerical taxonomy. W.H.Freeman and Company, San Francisco. 359pp.

WALKER, E.P. 1964. Mammals of the world. 2 Vols. The John Hopkins Press, Baltimore. 1500pp.

WEINER, J.S. and CAMPBELL, B.G. 1964. The taxonomic status of the Swanscombe skull. In C.D.Ovey (ed.), The Swanscombe skull, pp.175-209. Royal Anthropological Institute, 215pp.

WILLIAMS, W.T. and LANCE, G.N. 1965. Logic of computer-based intrinsic classifications. Nature, 207: 159-161.

WOOD, A.E. 1947. Rodents - a study in evolution. Evolution, 1: 154-162.