A Taxonomic Review and Phylogenetic Analysis of *Homo habilis*

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by

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ABSTRACT

Homo habilis is a late Pliocene to early Pleistocene hominid defined from a series of fossils found at Olduvai Gorge, Tanzania. Fossils from other hominid sites in eastern and southern Africa have been referred to H. habilis, yet the species is still poorly known. Specimens attributed to H. habilis sensu lato are quite variable in size and shape, and some authors have suggested that the hypodigm should now be subdivided. The aims of this study were first, to investigate whether the morphological variation among fossils attributed to H. habilis is consistent with known patterns of intraspecific variation, and second, to assess the phylogenetic relationship between H. habilis and other Plio-Pleistocene hominids.

The literature on H. habilis was reviewed and previous morphometric and systematic studies of the Hominidae were reappraised. Original measurements were taken on hominid and extant primate crania, mandibles and dentition. Anatomical structures known to be variable among hominids were selected for measurement, and measurements were defined strictly so that structures homologous between different species could be measured. The data were converted to logarithms, corrected for differences in overall size and then converted to dimensionless ratios using Kazmierczak's transformation.

Phenetic comparisons between individuals within extant primate species were undertaken using Mean Character Difference (MCD) as a measure of morphological distance. A maximum level of intraspecific variation in MCD was determined empirically for the primate species. This limit was then applied to the morphological variation within conventionally-defined hominid species, and it was shown that fossils attributed to H. habilis exhibited variation in shape in excess of that found in sexually-dimorphic primate species. H. habilis sensu lato was therefore subdivided into H. habilis sensu stricto, known only from Olduvai Gorge, and Homo sp., represented in this study by specimens from Koobi Fora, Sterkfontein and Swartkrans.

A cladistic analysis of hominid taxa was then undertaken, using the character state data that had been obtained for the study of intraspecific variation. This data was analysed with the PAUP maximum parsimony computer program, together with data for the extant primate outgroup. The most parsimonious hominid cladogram showed that while Homo sp. had cladistic affinities with the 'robust' australopithecines, H. habilis sensu stricto was placed as a plesiomorphous sister taxon to later species of Homo.

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CHAPTER 1: INTRODUCTION

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CHAPTER 1. INTRODUCTION

1.1 Introduction to some concepts

1.1.1 The species

The term 'species' is sometimes used in non-biological contexts to indicate a particular 'kind' or 'sort' of material object (for example, in chemistry a 'species' refers to a particular molecular configuration). In biology, the species is more narrowly defined, and in zoology in particular the definition is usually made with reference to reproductive criteria. Many biologists have adopted Mayr's 'biological species concept', in which the species is defined by two properties: reproductive isolation from other species, and genetic continuity within the species (Mayr, 1950, 1963). Mayr viewed the biological species concept as replacing the morphological and typological concepts of earlier biological taxonomies, although he acknowledged that some of those taxonomies also incorporated genetic or reproductive criteria (Mayr, 1963, p. 19). The reproductive or interbreeding criterion did, however, play an important role in the much earlier species definitions advanced by Buffon and Cuvier:

> "We should regard two animals as belonging to the same species if, by means of copulation, they can perpetuate themselves and preserve the likeness of the species; and we should regard them as belonging to different species if they are incapable of producing progeny by the same means."

(Buffon, 1749, p. 10; translation taken from Lovejoy, 1968).

> "Generation being the only means of ascertaining the limits to which varieties may extend, species should be defined the reunion of individuals descended one from the other, or from common parents, or from such as resemble them as closely as they resemble each other"

(Cuvier, 1863, p. 7 - emphasis in original).

A number of authors have discussed whether the interbreeding criterion can be 'operationalised' (i.e. whether it can be put into practice), particularly when considering the problem of identifying fossil species (see references in Wiley, 1978). Wiley has pointed out that the utility of the biological species concept does not depend on whether its axioms can be 'operationalised', but lies instead in the logical corollaries, or implications, that can be deduced from the biological definition of the species (Wiley, 1978; see also Eldredge & Cracraft, 1980). One consequence of reproductive isolation (and one which has a bearing on the question of identifying species) is that it tends to give rise to morphological discontinuity between the isolated units. According to Dobzhansky *et al.* (1977, p. 169): "....discontinuity and a hierarchical ordering are universal in the living world. They are the consequence of the fact that only a minority of the potentially possible gene combinations can give rise to viable organisms".

Systematists of different schools agree that morphological discontinuity is a suitable criterion for recognising species. For instance, Simpson stated "If the ranges of population variation (including polymorphy) inferred from two or more samples overlap for all observable characters, there is high probability that the corresponding populations were or had recently been interbreeding when the specimens were alive and that they therefore belong to the same genetical species." (Simpson, 1961, p. 151). Similar criteria have been advocated by numerical taxonomists: "The majority of taxa are definable because of the discontinuities arising in phyletic lines as a byproduct of the evolutionary process" (Sokal and Sneath, 1963, p. 10). Among cladists there are some (e.g. Vrba, 1980) who support the use of morphological discontinuity as a means of identifying species, while others, such as Wiley (1978) tolerate the morphological criterion only as a "working hypothesis", and yet others (notably Bonde, 1981) claim to have abandoned it altogether. (The implications of a cladistic definition of the species are explored in the following Chapter). In the present study, a morphological approach to species identification has been adopted. This approach is justified by the 'working hypothesis' that the limits of gene pools correspond to the limits of some quantitative measure of within-species morphological variation (cf. Babin, 1980).

The biological species was redefined in evolutionary terms by Simpson as "a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies" (Simpson, 1951, p. 289). This definition was, in turn, reframed in ecological terms by Van Valen: "A species is a lineage (or closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (Van Valen, 1976, p. 233).

These alternative definitions seem to be unnecessary, in that they appear to differ from Mayr's definition only by incorporating some of the implications that follow logically from his definition. Interbreeding, reproductively-isolated groups of organisms will (by implication) evolve, adapt and have their own evolutionary tendencies and fates; thus the redefinitions of Simpson (1951) and Van Valen (1976) seem to be redundant.

Recently, another definition of the biological species has been offered by Paterson (1978, 1980, 1981, 1982, 1985). According to Paterson (1985, p. 25) a species is "that most inclusive population of individual biparental organisms which share a common fertilization system". Paterson views both interbreeding and reproductive isolation as consequences of the shared possession, among a group of organisms, of a 'Specific-mate Recognition System' (SMRS). The properties of reproductive isolation and interbreeding, together with the expected morphological discontinuities between species, follow logically from Paterson's new definition: they are implied by the existence and shared possession of the SMRS. An additional implication of the new definition is that morphological aspects of the SMRS <u>itself</u> might be identified by the taxonomist, and thus assist in the determination of non-arbitrary boundaries among both living species (Ryan, 1986) and between species known only from the fossil record (Vrba, 1984; Turner, 1985, 1986).

1.1.2 Biological variation

If morphology is to be used as a means of identifying species and the boundaries between them then two further concepts need to be explored. These are the nature of morphological variation, and the means by which such variation might be measured or quantified.

Seilacher (1970) and Raup (1972) have discussed the major determinants of external biological form, but they made no distinction between intra- and interspecific variation. This distinction, between the morphological variation that occurs within a species and that which occurs between species, is emphasised here. There is not only a difference in degree between intra- and interspecific variation, but more importantly these different kinds of variation often have a different origin and have different roles in the adaptations of organisms and species respectively. For example, the hierarchical pattern of phenotypic similarity between species (the 'hierarchical ordering of Dobzhansky et al., 1977) is unlikely to be found among organisms within a species, in the absence of barriers to genetic exchange. The distinction also has empirical importance, as noted by Smith (1981) in his comparison between intra- and interspecific allometry equations, which differ in a fashion that is only partially explicable by the degree of size difference seen within and between species.

Within-species variation is primarily a property of individuals, rather than of subspecific populations. It has both intrinsic (genetic) and extrinsic (environmental) causes, and is generally adaptive in the physiological rather than in the evolutionary sense. Individuals within a species may vary according to their ontogenetic, sexual and racial/clinal status, and may, in addition to the above, exhibit stochastic or mutational variation. This variation has a genetic basis, but individual variation is also directly influenced by environmental factors: nutrition, pathology and ecophenotypic effects are examples. Furthermore, if a species is responding morphologically to directional selection its individuals (and, of course, the species as a whole) will vary as a function of time.

It is useful to regard between-species variation as a property of the species as a whole, as well as being a characteristic of the individual organism (c.f. Ghiselin, 1974 and Rieppel, 1986 for discussion of the individuality of species). Interspecific variation is exclusively genetic in its underlying control and largely adaptive (in the evolutionary sense) in its origin. Although this variation can itself be the subject of selection (so-called species-selection), between-species variation is more usually viewed as the product, rather than the raw material, of selection. The following categories of interspecific variation are recognised here:

a) Adaptive variation. Morphological differences between species that reflect species-specific adaptations to the environment.
b) Allometric variation. Morphological differences, of positive or neutral value, that primarily reflect interspecific differences in body size.
c) Pleiotropic variation. Features of neutral adaptive value that appear in a species because they are genetically correlated with other features that do have adaptive value for the species.
d) Plesiomorphic variation. 'Phylogenetic legacy', or features of

neutral adaptive value that are inherited from a common ancestor, but are differentially retained among descendant species.

e) Stochastic variation. A category which includes founder effects and differences due to genetic drift, where these have not been included under a) above.

In any morphometric analysis there are further sources of variation that are not properties of the individual organisms or the species to which they belong. I include here experimental error, and factors which affect sample selection, such as taphonomy and curatorial practice.

1.1.3 Morphometrics

Morphology, or form, has traditionally been divided into two components, size and shape (Gould, 1977). Gould has traced this distinction back to the writings of Aristotle (Gould, 1977, p. 236), but the division is implicit in the earlier Pythagorean distinction between the arithmetic and geometric properties of number (Guthrie, 1962). A number, when associated with a given unit of measurement, can express the size of a form. Dimensionless numbers, such as ratios (and angles, which are trigonometric ratios), are by definition not associated with units of size. They can, instead, be used to express simple shape attributes, for example robusticity (the ratio of the breadth of an object to its length). Outline forms of simple geometry, such as regular polygons and conic sections, can be described completely using only a few numbers. For example, an ellipse is described completely by two numbers representing the size of the ellipse and the ratio of its major and minor axes. More complex shapes, however, can in general only be approximately described by this numerical approach, and an adequate description of a complex shape might require the collection of a large amount of point coordinate data.

Biological forms achieve their shape through growth. One morphometric approach to the description of biological shape differences seeks to model these differences as resulting from differential growth. This technique, which is termed allometry, identifies scaling relationships between linear dimensions through bivariate regressions of logarithmically transformed measurements of objects that vary in size. While allometry identifies an aspect of shape that is dependent on size (in essence, growth-related shape differences - Sweet, 1980), size may make an unwanted appearance as a confounding variable in other techniques of morphometric analysis. A number of workers have stated that size is less meaningful than shape in taxonomic and phylogenetic studies (Penrose, 1954; Gould, 1966; Corruccini, 1973; N.A. Campbell, 1978; D.S. Wood, 1983; Reist, 1985), and the removal of the effect of size is often considered mandatory in comparative biometric studies.

A variety of methods of size correction or size removal are available (Corruccini, 1977; Atchley, 1978; D.S. Wood, 1983; Reist, 1985; Berge & Kazmierczak, 1986; Somers, 1986). These include normalisation (the conversion of variables to zero mean and unit standard deviation), the use of ratios (among variables, or between variables and a standard measure of size), the regression of specimens to a standard size and the use of residuals after size subtraction (references as above). A useful concept here is that of the shape function, which is invariant when all variables are changed in the same proportion (that is, the shape function is invariant to isometric change; Mosimann, 1970; Hills, 1978).

The simplest shape function (_sensu_ Mosimann and Hills) is a ratio of two linear measurements of a given form. However, the use of ratios in biometric studies has been criticised, both by biologists (Simpson _et al._, 1960; Gould, 1966; Blackith and Reyment, 1971) and by statisticians (Atchley _et al._, 1976). Simpson _et al_. (1960) gave vague warnings against the use of ratios ("Ratios...have, however, certain peculiar and generally ignored properties that must be kept in mind and may in some cases make conclusions based on them inaccurate or even invalid" - Simpson _et al._, 1960, p. 14). Atchley _et al._ (1976) levelled more specific indictments against the use of ratios: "ratios do not remove the effect of scaling variables but rather increase the correlation between the ratio variable and the original scaling variable" (Atchley _et al._, 1976, p. 137). The latter authors also commented on the non-normality of frequency distributions of ratio data.

The statistical difficulties posed by ratios and other shape functions may be more apparent than real. Atchley _et al._ (1976) reported high correlations between ratios and their component variables under two sets of artificial conditions, firstly when the coefficient of variation in the numerator variable greatly exceeded that of the denominator variable, and secondly when denominator and numerator were uncorrelated. This potential difficulty was rejected by Corruccini (1977), Albrecht (1978), Dodson (1978) and Hills (1978), who pointed out that these conditions are unlikely to arise in biological applications of ratios. The further difficulty identified by Atchley et al. (1976) lay in the non-normality of frequency distributions of ratio data, and in the non-linearity between a ratio and its component variables. The latter problems disappear after logarithmic transformation (Hills, 1978) since the log-transformed ratio is a linear function of its log-transformed component variables. In algebraic terms, the logarithm of a ratio is equal to the arithmetic difference between the log-transformed variables; for the ratio a/b, Log (a/b) = Log (a) - Log (b).

The complexity of biological forms has led many biometricians to adopt multivariate methods of comparison and discrimination. A variety of such techniques are available (Howells, 1984), but the method of choice has often been multiple discriminant analysis (also known as canonical variates analysis, or CVA) together with its associated metric, generalised or Mahalanobis distance (D^2). Mahalanobis distance is a parametric statistic that provides a measure of similarity of groups or of individuals that takes into account both variance and covariance among the variables in the analysis (Corruccini, 1975a; N.A. Campbell, 1978). The valid use of both CVA and D^2 is dependent on the assumption that the specimens or groups belong to populations with the same variance-covariance matrix (N.A. Campbell, 1978, refers to this as the 'assumption of homogeneity of covariance'). Although Blackith & Reyment (1971) minimise the importance of covariance homogeneity, other authors emphasise that violation of this assumption has more serious consequences than other departures from multivariate normality (Corruccini, 1975a; N.A. Campbell, 1978). The accurate estimation of the covariance matrix is essential to the calculation of D^2, which generally requires that large samples of specimens are taken from the same species or from a series of morphologically similar taxa (Cherry _et al._, 1982). Van Vark (1984) overcame the problem of small sample sizes in hominid studies by deriving his variance-covariance matrix from a large sample of modern human specimens. There remains the problem of testing the equality of the variance-covariance matrices among different hominid populations. Van Vark (1984) found no significant differences in variance-covariance among Mid-Pleistocene to Holocene hominid groups, but noted that because of small sample sizes "Even if important differences should exist, they would not easily be detected" (Van Vark, 1984, p.339). Rightmire (1969) stated that covariance assumptions have been subjected to 'extensive testing' with 'encouraging results', but such tests appear to involve comparisons of populations _within_ a single species (anatomically-modern _Homo sapiens_). In a study by Cherry _et al._ (1982), in which different measures of interspecific morphological distance were compared, D^2 proved unreliable, apparently because of covariance matrix inhomogeneity across the wide range of taxa in their study.

An alternative approach to the quantification of a complex shape is to code or score individual components of the shape in a standardised fashion. These individual components are referred to as 'characters', and each character can be binary coded (present/

absent), or can take a value on a scale reflecting different degrees of expression of the character. This approach is common in taxonomy, and has also been used to record 'non-metric' skeletal traits for population genetic studies of humans and other animals (Berry, 1979). Sophisticated multivariate statistical techniques for comparing individuals and groups using non-metric traits are reported to be under development (Finnegan and Rubison, 1984).

1.1.4 Homology

Homology is the fundamental principle underlying comparisons between biological structures: "Homology is the central concept in anatomy" (Van Valen, 1982, p. 305). Van Valen defines homology in terms of its causes: "Homology is resemblance caused by continuity of information" (Van Valen, 1982, p. 305). Under this general definition are subsumed two different kinds of homology. Historical, or phyletic homology refers to the resemblance between structures present in different species, whereas repetitive, or serial homology refers to resemblance between different structures within the same organism (a similar distinction is made by Ghiselin (1976) and Roth (1984)). According to Van Valen, these different kinds of homology have a common cause - continuity of information - and he argues that the distinction between historical and repetitive homology is arbitrary and 'fuzzy' (Van Valen, 1982, p. 307).

Patterson (1982) has also discussed the concept of homology, and his arguments stand in very marked contrast to those of Van Valen (1982).

Patterson defines homology in terms of monophyly: homologous features are those which characterise a monophyletic group, and are, in fact, synapomorphies of that group (Patterson, 1982). For example, the different kinds of mammalian fur are homologous: this homology (fur) is one of the synapomorphies that define mammals as a monophyletic group.

Patterson distinguishes homology from homoplasy (parallelism and convergence) by invoking three tests of homology: the tests of 'similarity', 'conjunction' and 'congruence'. The test of similarity, that homologous features should resemble one another in their anatomy, developmental history etc., is the least rigorous test, and discriminates poorly between homology and non-homology. The test of conjunction is more rigorous - it excludes any assumption of homology between different features of two organisms if those features can be shown to coexist ('conjunction') in a third organism. The third, and most reliable test of homology is that of congruence, or agreement with other evidence. Homologies, according to Patterson, define monophylies, and it thus follows that a test of any hypothesis of homology would be to demonstrate 'congruence' with the monophylies defined by other homologies. These congruent homologies stand in hierarchical relationship to the first homology; they define the same monophyletic group, or a subset of it, or a larger group that wholly contains it. 'Congruence' is identical to the concept of 'consistency' developed by phylogenetic systematists (e.g. Kluge and Farris, 1969), and any conflicts between incongruent homologies can presumably be resolved by invoking criteria of parsimony.

Patterson's definition of homology excludes the category of repetitive, or serial homology recognised by Van Valen (1982). Patterson (1982) uses the separate term 'homonomy' to refer to so-called 'anatomical plurals', that is structures such as red blood cells or nuclear DNA that occur as multiple copies within any one organism. Patterson regards statements of serial homology (for example, proposed homologies between similar anatomical structures in the tetrapod fore- and hindlimb) as untestable hypotheses of homonomy. By this he presumably means that if the serial structures were truly homonomous they would be given the same name, and that it is often difficult (or arbitrary) to decide whether complex serial structures are sufficiently similar to warrant their receiving the same name.

1.1.5 Phylogeny and its reconstruction.

A phylogeny is a representation of the pattern of descent of a group of taxa from their common ancestor. The method of phylogenetic reconstruction followed in the present study is known as phylogenetic systematics (Hennig, 1950, 1965) or cladistics (Cain and Harrison, 1960; Mayr, 1965). The term cladistics has been applied both to methods of estimating the branching sequence of a group of taxonomic units, and as a means of classifying them (Mayr, 1974). In the present study the term is used in the former (phylogenetic) rather than in the latter (classificatory) sense.

Cladistics is a method for reconstructing phylogenetic history using morphological resemblance between taxonomic units (Hennig, 1965). Other methods of phylogenetic reconstruction, including phenetics (Sokal and Sneath, 1963; Mayr, 1965), stratophenetics (Gingerich, 1977, 1979) and evolutionary systematics (Mayr, 1969, 1974) also use morphological resemblance as a criterion of relatedness among taxa. Cladistics is distinct from these methods, however, in its partition of the morphological resemblance between any pair of taxa into a part which is inherited from their most recent common ancestor (synapomorphy) and a part that is inherited from more distant ancestors (symplesiomorphy) or that has arisen independently in separate lineages (convergence). In the cladistic method, only morphological resemblance that can be inferred to have been inherited from a most recent common ancestor (i.e. synapomorphic resemblance) can be used as evidence for phylogenetic relatedness between taxa. In the cladistic method, relatedness equals recency of common ancestry.

The synapomorphies identified among a group of taxa form a nested pattern among those taxa; some synapomorphies indicate an exclusive relationship between just two taxa, while others delineate larger clusters of taxa. The overall, synoptic pattern of the synapomorphies is represented on a tree diagram, or cladogram. The individual taxa are placed as terminal branches on the cladogram, and their phylogenetic branching sequence is depicted in the branching structure, or topology, of the cladogram. Conflicts that arise between synapomorphies, where different synapomorphies indicate incompatibly different patterns of relationship among taxa, can usually be resolved by invoking the criteria of parsimony (the Wagner criterion - Farris, 1970) or compatibility (Le Quesne, 1969).

A fundamental distinction between cladistic and phenetic methods has been identified by Penny (1982). Both methods start with a matrix of taxa and their character states (Figure 1.01). This 'character state matrix' is of order n x c, where n is the number of taxa and c is the number of characters. Phenetic methods convert this n x c matrix into an n x n matrix of proximities between taxa, and then use a clustering algorithm to extract any hierarchical pattern among the proximities. Cladistic methods, on the other hand, aim to find the shortest possible sequence of character state changes that explain the complete data set (i.e. the data represented in the original n x c matrix).

Compatibility analysis is a variant of the cladistic method in which characters are weighted according to their respective consistency indices (Le Quesne, 1969, 1974, 1982; Estabrook et al., 1977). Compatibility analysis identifies groups of characters that are 'mutually compatible', so that each group defines a tree that is apparently free from homoplasy. The tree defined by the largest group of mutually compatible characters may be chosen as the correct tree, while trees defined by smaller clusters of characters are regarded as reflecting the false patterns of similarity produced by convergence, reversal and parallelism.

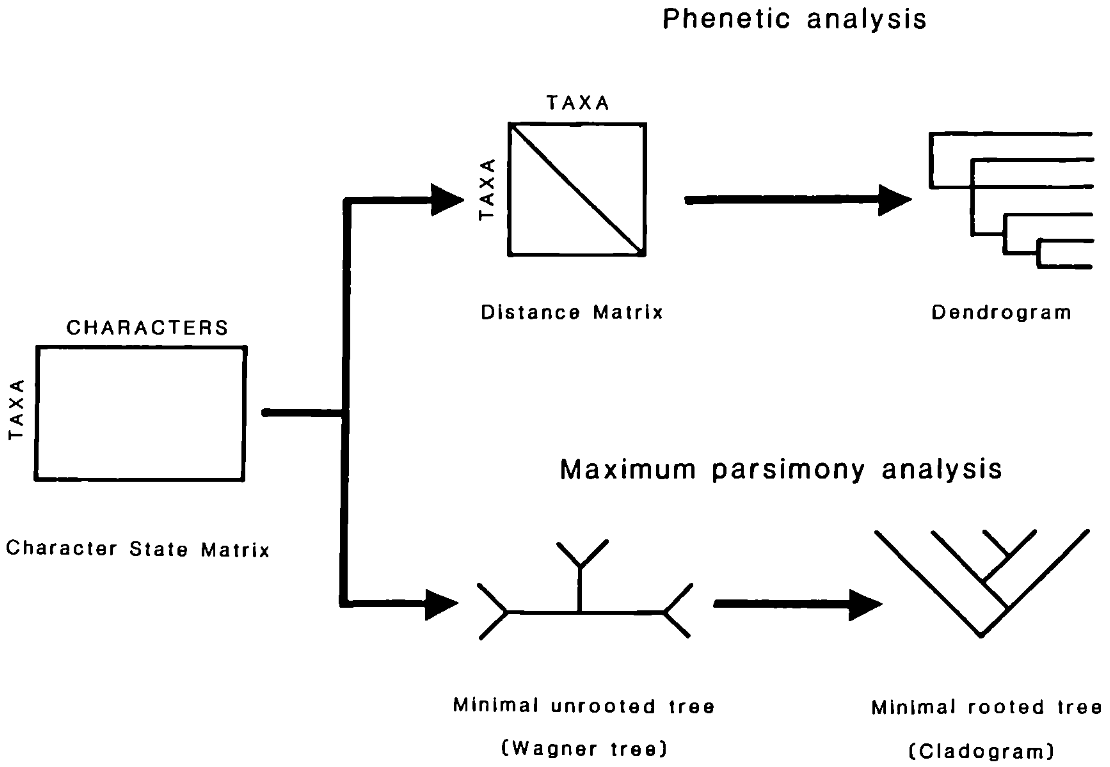


Figure 1.01 Distinction between phenetic and cladistic analysis (after Penny, 1982)

1.2 Introduction to hominid systematics

1.2.1 Definition of hominids.

Conventionally, the term 'Hominids' refers to a group of animal species, mostly extinct, that are closely related to each other and to modern humans, and are broadly ancestral only to modern humans among living primates. Taxonomically, however, Hominidae is defined as the family containing the type genus *Homo*. In taxonomic terms, a family is a group of genera that are similar to each other and distinct from genera of other families. Among the living primates, the genera most similar to *Homo* are the African great apes *Pan* and *Gorilla*. These genera have almost always been considered to be morphologically distinct from modern humans, and have usually been placed in a separate family, either Pongidae (including the Asian great ape *Pongo*), or Panidae (excluding *Pongo*) (Simons, 1972; Ciochon, 1983). The evidence provided by studies of molecular similarity among primates suggests that there is a very close phylogenetic relationship between the African great apes and modern humans (Goodman, 1961; Hasegawa *et al.*, 1984; Sibley and Ahlquist, 1984; Miyamato and Goodman, 1986). Some authors have therefore included *Pan* and *Gorilla* in a subfamily (Paninae, or Gorillinae) within Hominidae (Andrews and Cronin, 1982; Richard, 1985), or have even included all three genera, *Pan*, *Gorilla* and *Homo* in the same subfamily Homininae (Goodman, 1986; Groves, 1986). These nomenclatural changes have received some recognition among neontologists, but have not yet been widely accepted by hominid palaeontologists (c.f. Martin, 1986).

For the purposes of the present study, the family Hominidae is defined cladistically - it includes those taxa which form a monophyly containing only one extant species, Homo sapiens. In phylogenetic terms, it includes all species whose common ancestor is more closely related to Homo sapiens than to any other living primate.

1.2.2 Defining characters of hominids

A suite of genetic, developmental, morphological, physiological, ecological, behavioural, cognitive and cultural characters support a distinction between Homo sapiens and all other primates (Lovejoy, 1981; Tooby and DeVore, 1987). These characters are apomorphic in Homo sapiens, but whether they are shared with other hominids is, in many instances, unknown. For the palaeontologist, the only useful defining characters for hominids are those which are preserved in the fossil record. Such characters are predominantly skeletal ones, but they are supplemented by a limited number of soft tissue characters, as evidenced for example by natural cranial endocasts and fossil footprints. In addition, there is some fossil evidence for material culture, including stone tools and processed faunal remains.

The fossil record yields evidence for at least three major morphological adaptations that appear to be confined to hominids. These adaptations involve changes in posture and mode of locomotion, in the masticatory system and in encephalisation (Lovejoy, 1981). Evidence for erect posture and bipedal locomotion is seen in characters of the axial and appendicular skeleton of fossils (Robinson, 1970, 1972b; Day, 1986a), and in fossil footprints (M.D. Leakey and Hay, 1979; M.D. Leakey, 1981; Behrensmeyer and Laporte, 1981). A suite of dental and cranial characters, including canine reduction, 'molarisation' of the premolars, restructuring of the dental arcade and of the pattern of mandibular buttressing, are evidence that hominids shared a derived masticatory system (Johanson and White, 1979). Calculations of cranial capacity and relative brain size, together with studies of endocast morphology indicate that enhanced encephalisation and a degree of structural reorganisation of the brain was shared by all hominids (Holloway and Post, 1982; Holloway, 1983a).

1.2.3 Species and genera of hominid

The majority of hominid palaeontologists recognise two genera of hominids, *Australopithecus* and *Homo*. A few workers argue that the Miocene form *Ramapithecus* should be included in the Hominidae, either as a distinct genus or as part of the genus *Sivapithecus* (de Bonis, 1983; Kay and Simons, 1983; Oxnard, 1984). A more prevalent view, however, is that the apparent dental similarities between *Ramapithecus* and *Homo* reflect parallelism and convergence between phylogenetically separate lineages (Andrews, 1978). For example, thick dental enamel can be viewed as a parallelism (symplesiomorphic character) in *Ramapithecus* and *Homo*, having been retained from an ancestral large-bodied hominoid (Martin, 1985). Furthermore, if *Ramapithecus* is synonymous with *Sivapithecus*, the affinities of this hominoid may lie with the Asian great ape *Pongo* (Andrews and Cronin, 1982; Ward and Pilbeam, 1983) rather than with the Hominidae. Finally, biomolecular studies suggest that the African great apes diverged from the hominids at the end of the Miocene, or in the early Pliocene. Thus most of the Miocene fossils represent populations that predate the divergence of the African apes, and such fossils must therefore be excluded from the Hominidae as defined above.

The genus *Australopithecus* includes the following genera as junior synonyms; *Plesianthropus* Broom, 1937, *Paranthropus* Broom, 1938, *Zinjanthropus* Leakey, 1959 and *Paraustralopithecus* Arambourg and Coppens, 1967. Four species of *Australopithecus* are currently accepted by most workers, two 'gracile' species *A. africanus* and *A. afarensis*, and two 'robust' species *A. robustus* and *A. boisei*. A few workers recognise a third 'robust' species *A. crassidens* (Howell, 1978; Grine, 1984), and recent discoveries in East Africa suggest that a further 'robust' species of *Australopithecus* might be represented in the fossil hominids from that region (Walker *et al*., 1986; Delson, 1986, 1987). The case for retaining *Paranthropus* as a separate genus for the 'robust' species of *Australopithecus* has been reinforced by the results of recent studies (Olson, 1985; Dean, 1986; Wood and Chamberlain, 1986; Chamberlain and Wood, in press), but has yet to achieve widespread acceptance among hominid palaeontologists.

The type genus of the Hominidae, *Homo*, incorporates as junior synonyms several generic nomina that were erected to accommodate a range of fossil forms. These sunk genera include *Pithecanthropus* Dubois, 1894; *Sinanthropus* Black, 1927; *Meganthropus* Weidenreich, 1945 and *Telanthropus* Broom and Robinson, 1949. *Homo* currently includes three species, *H. habilis*, *H. erectus* and *H. sapiens*. Most workers recognise subspecific categories for fossil forms of *H. sapiens* (cf. Howell, 1978), but such subdivisions are less clearly delineated among remains attributed to *H. habilis* and *H. erectus*. The latter two species include forms that a minority of authors attribute to distinct species (Groves and Mazak, 1975; Bilsborough, 1976; Franzen, 1985), and it is generally recognised that fossil species of *Homo* exhibit a high degree of morphological heterogeneity (Bilsborough, 1976; Wood, 1985a, 1985b; Stringer, 1986; Chamberlain and Wood, in press).

1.2.4 Distribution in time and space

The extinct genus *Australopithecus* is known from Late Pliocene to Lower Pleistocene fossil sites along the East African Rift Valley system and in the Transvaal. There is no convincing evidence for the presence of the genus at sites outside the continent of Africa. Faunal and radiometric dating of sites at which *Australopithecus* occurs indicates that the 'gracile' species predated the 'robust' ones (White and Harris, 1977; Schmitt and Nairn, 1984; Brown *et al.*, 1985a; Jones *et al.*, 1986). At no site is there compelling evidence for the presence of more than one contemporaneous species of *Australopithecus*, but in both eastern and southern Africa the 'robust' species appears to have been contemporaneous with early species of *Homo*, namely *H. habilis* and *H. erectus* (Howell, 1978).

The type site of H. habilis is Olduvai Gorge, Tanzania, but material from a number of Early Pleistocene fossil sites in eastern and southern Africa has also been referred to this species. H. habilis has not been detected at sites outside the African continent. H. erectus has been found in East Africa in deposits that have been dated radiometrically to about 1.6 Myr BP. The type site of H. erectus, at Trinil, Java, is one of a number of Asian occurrences of this species, all of which are now estimated to date from less than 1.3 Myr BP (Matsu'ura, 1982; Hooijer and Kurten, 1984; Sondaar, 1984). Some fossil hominids from Europe have also been referred to H. erectus, but there is considerable disagreement over the taxonomic affinities of these European specimens, which may instead represent an 'archaic' subspecies of H. sapiens (Stringer, 1981).

Three taxonomic subdivisions of H. sapiens are recognised in the present study. These subdivisions distinguish between anatomically modern H. sapiens and two distinct fossil forms, 'archaic' H. sapiens and H. sapiens neanderthalensis. The morphological differences between these forms are reported to be much greater than those seen between even the most morphologically distinct populations of modern H. sapiens (Stringer, 1974). Taxonomic subdivision of modern H. sapiens is invalidated by the results of studies of genetic variation within and between modern human populations. Such studies show that only a small proportion of modern human genetic variation is accounted for either by differences between morphologically-defined 'races' or by differences between geographically circumscribed populations (Lewontin, 1972; Latter, 1980).

1.2.5 Relationships among hominids

Hominid phylogeny is perhaps the area in which the least consensus exists among hominid palaeontologists. This lack of consensus has been a feature of hominid systematics for over one hundred years (Brace, 1981), and persists to the present day despite the recent application of rigorous methods of phylogenetic analysis to extensive samples of fossil hominids (e.g. Kimbel et al., 1984; Skelton et al., 1986; Wood and Chamberlain, 1986; Chamberlain and Wood, in press). Brace attributed the current arguments over hominid phylogeny to the persistence of different intellectual traditions among hominid palaeontologists: "the interpretive styles of a century ago are still with us in several guises" (Brace, 1981, p. 423). There is, however, a simpler, and, in my view, more plausible explanation. This is that the resolution of hominid phylogeny is a particularly difficult problem in systematics. There is no a priori reason to believe that the source of the problem lies with any presumed inadequacy of the hominid fossil record, for the phylogenies of other mammalian groups, with comparable fossil records, have been resolved satisfactorily using cladistic methods. Examples include Miocene Giraffoids (Hamilton, 1978), Miocene-Recent Alcelaphines (Vrba, 1979a) and African Plio-Pleistocene Suidae (Harris and White, 1979). Thus, by implication, the discovery of additional fossil hominid material is not, of itself, guaranteed to improve our current resolution of hominid phylogeny.

There are several reasons why hominids as a group might be refractory to phylogenetic analysis. Firstly, hominids belong to an animal order, primates, which as a group present problems for morphologically-based methods of phylogenetic reconstruction. Groves has alluded to this: "Taking the mammals as an example, it is probably fair to say that the internal arrangement of most orders is widely accepted, only the Rodentia, Insectivora and Primates being sources of major disagreement" (Groves, 1974, p.449). These three orders are all relatively unmodified in their general structure, preserving a number of primitive mammalian characters of the locomotor and masticatory systems. Problems in resolving the phylogenies of these orders might thus be attributed to a lack of highly diagnostic, or derived characters.

Secondly, modern humans, and perhaps other hominids, are distinguished among primates by their neoteny, which affects a series of morphological characters and which is perhaps attributable to a single process, that of ontogenetic retardation (Gould, 1977). Neotenic characters appear as reversals in any character phylogeny (Eldredge and Cracraft, 1980; Bonde, 1984) and therefore have the potential to confound any attempt to resolve phylogeny. Creel (1986) identified human neoteny as a confounding factor in his attempt to reconstruct the phylogeny of the extant hominoids using cranial morphometric data.

A third reason why hominid phylogeny might be difficult to resolve may lie in the possession, by at least some hominids, of material culture and language. Human culture has been defined by White as man's extrasomatic adaptation to his environment (White, 1959, p. 8), a definition which extends easily to any culture-bearing hominid.

Mayr (1950) and Robinson (1954) noted that cultural adaptation may be a deterrent to speciation, and Turner (1985) has commented that the appearance of language may have heralded a shift from a visual (and hence morphological) SMRS. Any attempt to map out hominid phylogeny on the basis of morphological characters should bear in mind the possibility that some of the principal hominid adaptations may be cultural, rather than morphological.

Despite this pessimistic assessment, there is every reason to believe that phylogenetic information is preserved in the morphology of fossil hominids, and that rigorous attempts to extract such information should be made. Even if one accepted the proposition (B.G. Campbell, 1978, for example) that divisions between hominid taxa are arbitrary (which I argue against - see above), there are no grounds for accepting subjective or arbitrary statements about hominid phylogeny. For any group of animal species there is only one true phylogeny, and our methods of phylogenetic reconstruction should aim to recover it.

1.3 Introduction to the problem

1.3.1 Evolution within *Homo*, and the status of *Homo habilis*

Debate in hominid systematics includes the pattern of evolution within the genus *Homo*. Prior to 1964, a unilineal pattern of descent from *Australopithecus*, through *H. erectus* to *H. sapiens* was generally accepted among palaeontologists. According to Le Gros Clark, this 'working hypothesis' was based on the morphological and chronological intermediacy of *H. erectus* between *Australopithecus* on the one hand and *H. sapiens* on the other. The intermediate position of *H. erectus* was supported by the existence of a series of fossil specimens, themselves of intermediate form, linking *H. erectus* with *H. sapiens* (Le Gros Clark, 1964b, p. 116). When L.S.B. Leakey, Tobias and Napier (1964) proposed that an early form of *Homo* found at Olduvai Gorge, Tanzania, deserved recognition as a new species, *H. habilis*, they were, in effect, challenging this working hypothesis. Some anthropologists (including Le Gros Clark, and Robinson) viewed the new material from Olduvai as being truly morphologically intermediate between *Australopithecus* and *H. erectus*, and preferred to attribute the specimens to one or another of these existing taxa. The small collection of specimens from Olduvai Gorge was quite variable in morphology (both size and shape), with the inevitable result that some specimens appeared more like *Australopithecus*, while others were closer to *H. erectus* in form (cf. Robinson, 1965).

Since 1964 additional, more complete, hominid fossils from sites in eastern and southern Africa have been referred to *H. habilis* (Howell, 1978). Few workers argue that these specimens represent known species of *Australopithecus*, or *H. erectus*. However, the morphological variability of this material is appreciable (Wood, 1976a, 1978a) and has led some scientists to propose that the *H. habilis* hypodigm should be taxonomically subdivided (Groves and Mazak, 1975; Wood, 1978a; Stringer, 1986). Others maintain that such subdivision is unwarranted, and that the *H. habilis* hypodigm is characteristic of a single species possessing a marked degree of sexual dimorphism (cf. Howell, 1978).

The potential implications of subdividing *H. habilis* into two distinct species are considerable, and may explain why such subdivision has only been proposed by a few authors, and has not yet been achieved in a fashion that has received widespread support. The morphological distinctions on which such subdivisions have been based appear to be present among the specimens from each of the main *H. habilis* sites, Olduvai Gorge, Tanzania and Koobi Fora, Kenya. Furthermore, the same morphological distinctions can be made among specimens from within individual geological members at Koobi Fora, and within individual Beds at Olduvai Gorge. If *H. habilis* were to be subdivided in the fashion proposed by some authors, the separate taxa would have been contemporaneous, and by inference sympatric, at both of the sites where the evidence is most complete. Only one of the resulting taxa could be regarded as being ancestral to later forms of *Homo*, and perhaps only one taxon would have been responsible for the cultural evidence which is often associated with the fossil remains of these hominids.

The retention of a single taxonomic category for the diverse range of fossils presently included in the hypodigm of *H. habilis* presents its own problems. Of all the sources of intraspecific variation (see above), sexual dimorphism, it has been argued, is the most probable reason for the morphological variation within *H. habilis*. If the variation in *H. habilis* is to be attributed largely to sexual dimorphism then this hominid would have been more dimorphic in size than the extant great apes *Gorilla* and *Pongo* (Wood, 1985b; Lieberman, 1986), animals which are towards the top of the range of dimorphism exhibited by extant primates (Clutton-Brock *et al*., 1977). Moreover, much of the pattern of dimorphism between the proposed sexual morphs of *H. habilis* runs counter to established patterns of dimorphism in primate crania (Lieberman, 1986).

These problems are not unique to *H. habilis* among known hominid taxa. Other species, for example *A. boisei* and *A. afarensis*, are characterised by a large amount of morphological variation, although the case for sexual dimorphism in these hominids appears to have been argued more successfully than it has been for *H. habilis* (Kimbel *et al.*, 1984; Chamberlain and Wood, 1985). Some workers have argued for a taxonomic distinction between African and Asian forms of *H. erectus* (Andrews, 1984), but others, while recognising population or clinal differences, reject even subspecific distinctions within this species (Thorne and Wolpoff, 1981; Rightmire, 1984). The taxonomic status of *H. habilis*, however, is less secure than either that of *A. afarensis* or *H. erectus*; there are few who are prepared to defend the taxonomic integrity of the current hypodigm of *H. habilis*.

The integrity, then, of H. habilis as a single, species-level taxon has been questioned, but a consensus on the taxonomic subdivision of this species has yet to appear. A complicating factor is that monographic treatment of the two major collections of fosil hominids germane to H. habilis (from Olduvai Gorge, Tanzania, and Koobi Fora, Kenya) is in progress (Tobias, in preparation; Wood, in preparation). These publications will doubtless make a significant contribution to clarifying the taxonomic status of H. habilis, but there is no guarantee that the results and conclusions of their independent analyses of separate data sets will be compatible with each other. Nonetheless, the present study has been undertaken with the knowledge that more senior workers in this field have a keen, and prior, interest in the material under investigation.

For this reason, the present study should be viewed as an attempt to develop and apply a set of methods and criteria that will be applicable to taxonomic and phylogenetic problems in general. The application of these methods to the particular problems engendered by H. habilis should concomitantly be regarded as a trial of these methods, and that it is the wider applicability of these methods, rather than any consequences for hominid taxonomy and phylogeny, that are of primary importance.

1.3.2 Aims and approach of the present study

The aims of this study are to test, using quantitative criteria, the hypothesis that fossil specimens that are conventionally assigned to the species H. habilis represent a single species, distinct from other known hominid species. Regardless of whether the above hypothesis stands or falls, it is the further intention in this research to reassess the phylogenetic relationships between hominid species, using rigorous and quantitative methods of cladistic analysis. Indeed, one of the reasons for choosing to investigate both the taxonomic allocation of specimens and the phylogenetic relationships among taxa is to demonstrate to what degree the latter are influenced by the former.

In undertaking this study, with the above aims in mind, an implicit choice had already been made between a 'tabula rasa' or inductive approach, and one in which one or more hypotheses were to be subjected to critical appraisal. Since I was given the opportunity to collect a large amount of data from the original specimens, the former approach could have been chosen. The latter, 'hypothetico-deductive' approach was, however, adopted in preference to the former, in part for personal reasons, but largely in view of the following fact. H. habilis, as I hope to demonstrate in the following Chapter, refers to a small collection of palaeontological specimens about which a large number of written statements have already been made. It would be as pointless to ignore all of these (albeit to some extent contradictory) contributions as it would be to uncritically accept any one of them.

In reviewing the previous literature on H. habilis I have tried to be comprehensive rather than exhaustive, and I have placed particular emphasis on papers written by workers familiar with the fossil evidence for H. habilis, or by those with an established research interest upon which this fossil evidence has an important bearing. From the written evidence I have tried to gauge, subjectively, to what extent the hypotheses and statements that have been made about this species can be tested against quantitative evidence taken from the fossils themselves. In selecting measurements (all morphometric methods are, in effect, selective) I have again been guided by the literature. For example, I have rendered in quantitative form several of the aspects of cranial morphology that other workers (e.g. Howell, 1978) have used to distinguish between hominid species. In my approach to morphometrics, however, I review the standard methods and then largely abandon them, in favour of methods that are specifically designed to deal with the particular problems posed by incomplete fossils of unknown taxonomic attribution. Another aspect of my approach (but one that is not new) is to use the morphological variation in extant species of primate as a guide to the variation to be expected in fossil hominid species.

The approach to phylogenetic reconstruction that is used in the present study is a cladistic one. Again, the literature on this subject is reviewed, and both the methods adopted here, and the programs used to implement them, are widely available and have been used by many workers.

CHAPTER 2: REVIEW OF EARLIER WORK

2.1 Review of Homo habilis

2.2. Comments on hominid morphometrics

2.3 Comments on hominid systematics

CHAPTER 2: REVIEW OF EARLIER WORK

2.1 Review of Homo habilis

2.1.1 H. habilis defined

Following the discovery at Olduvai Gorge in July 1959 of Zinjanthropus (OH 5 - now the type specimen of Australopithecus boisei), further excavations in Bed I yielded the remains of a second type of hominid. A preliminary report of this material (L.S.B. Leakey, 1960) recorded cranial remains (OH 6) and a tibia and fibula (OH 35) from locality FLK (the original Zinjanthropus site), together with cranial remains and hand bones (OH 7), a foot (OH 8), two 'clavicles' (OH 48, and a fragment of a radius - OH 49) and two ribs (OH 50) from a second Bed I locality, FLK NN. A mandible and parietals belonging to OH 7 were subsequently recovered at FLK NN, and a preliminary description of these latter remains, together with a tentative discussion of their morphological affinities, were published (L.S.B. Leakey, 1961a). A second paper in the same year (L.S.B. Leakey, 1961b) gave measurements of the OH 7 dentition, emphasised the specimen's distinctiveness from Australopithecus, and suggested its affinity to Homo. A detailed description of the OH 7 hand bones identified them as belonging to an adult and a juvenile of the same species (Napier, 1962). In his paper Napier noted some morphological differences between the OH 7 juvenile hand and that of modern H. sapiens, but concluded that the OH 7 hand was anatomically capable of constructing the stone tools recovered from Bed I. Napier was, however, reluctant to refer OH 7 to Homo since there was no evidence that OH 7 had the intellectual or cultural status that he regarded as a necessary condition of membership of the genus *Homo*.

Tobias (1964a) estimated the cranial capacity of OH 7 as falling in the range 643-724 cc., and noted that the lower limit of his estimates was nonetheless larger than the capacity of any known australopithecine cranium. Davis (1964) gave a detailed anatomical description of the OH 35 tibia and fibula, and proposed that while the ankle joint of this individual was well adapted to bipedalism, the marked difference from anatomically modern man in the insertion of *popliteus m*. was evidence for a less complete adaptation at the knee joint than is seen in modern *H. sapiens*. Day and Napier (1964) described the OH 8 foot, emphasising its affinities to modern *H. sapiens* rather than to extant anthropoid apes. They also noted that the OH 8 talus resembled an australopithecine talus from Kromdraai, and that the distribution of robusticities in the metatarsals of OH 8 differed from the pattern seen in modern *H. sapiens*.

Continued excavation and collection at Olduvai Gorge, predominantly in Bed II, yielded further hominid material (OH 12 to OH 16) which was reported in L.S.B. Leakey and Leakey (1964). Two of these specimens (OH 13 from Lower Middle Bed II and OH 16 from Basal Bed II) were described as being cranially and dentally similar to OH 7 from Bed I. Following the recovery of this new material, L.S.B. Leakey *et al*. (1964) revised the definition of the genus *Homo*, and erected a new species, *Homo habilis*, to accomodate the majority of the new hominid material. The OH 7 mandible, parietals and hand bones were designated the holotype of the new species, and the description was based on these together with the paratype specimens OH 4 (mandibular fragment), OH 6 (cranial fragments), OH 8 (foot bones, together with two adult hand bones initially catalogued under OH 7) and the OH 13 cranium from Bed II. In the same publication two additional crania from Bed II, OH 14 and OH 16, were referred to the new species.

In L.S.B. Leakey *et al*. (1964) the revised definition of *Homo* extended the range of variation in that genus while maintaining, for a few cranial characters, morphological distinctiveness from *Australopithecus* (sensu Le Gros Clark, i.e. including the sunk genera *Paranthropus* and *Zinjanthropus*). A small amount of overlap between the two genera was to be allowed in cranial capacity, but *Homo* differed from *Australopithecus* in the following characters:

a. Lack of marked post-orbital constriction in the frontal region.
b. Absolutely smaller molars.
c. Front teeth not small relative to cheek teeth.
d. Teeth not bucco-lingually enlarged.

Many more characters were included in the revised definition of *Homo*, but these served principally to discriminate between *Homo* and the extant species of great ape, rather than between *Homo* and *Australopithecus*. In their definition of *H. habilis* the authors were concerned to distinguish their species from members of *Australopithecus* on the one hand and from other species of *Homo* (namely *H. erectus* and *H. sapiens*) on the other.

H. habilis differed from members of *Australopithecus* in having:

a. Smaller mandibles and maxillae.
b. Bucco-lingually narrowed premolars.
c. Large canine relative to premolar size.

H. habilis differed from *Australopithecus* and *H. erectus* in having:

a. Larger incisors.
b. Buccolingually narrowed and mesiodistally elongated lower premolars and molars.
c. Less marked external sagittal curvature of the occipital bone.
d. Cranial capacity intermediate between the two taxa.

There were no characters in which *H. habilis* differed from *H. erectus* while resembling *Australopithecus*, but there were several characters in which *H. habilis* differed from *H. sapiens* while resembling (or at least not having been shown to differ from) other hominid taxa. These characters were:

a. Lack of a bony chin.
b. Presence of muscle ridges on the cranium.
c. Larger molars.
d. Robust, dorsally-curved hand bones.
e. Placement of the distal attachment of flexor digitorum superficialis.
f. Stronger fibro-tendinous markings on the hand bones.
g. The orientation of the trapezium.

h. The form of the scaphoid.

i. The depth of the carpal tunnel.

j. The pattern of robusticities in the foot bones.

k. The form of the talar trochlea.

In addition to the characters listed above, it can be inferred from the revised definition of *Homo* that *H. habilis* differed from members of *Australopithecus* in possessing reduced post-orbital constriction and smaller molars.

2.1.2 *H. habilis* defended

Later in 1964 Tobias and Koenigswald had the opportunity to make direct comparisons between some cranial specimens of *H. habilis*, a cast of the Telanthropus I mandible from Swartkrans and some of the hominid jaws and teeth from Sangiran (Tobias and Koenigswald, 1964). Tobias withdrew from *H. habilis* the referred Bed II specimen OH 16 in view of its dental resemblance to *Australopithecus* (Tobias and Koenigswald, 1964 p.515). OH 13 (the other Bed II specimen in their comparative study) was retained in *H. habilis*, although it was noted that this specimen resembled Telanthropus I and the Javan specimens Pithecanthropus IV (upper jaw) and Sangiran B (mandible). The Bed I specimens, on the other hand, appeared to be taxonomically distinct from both *Australopithecus* and *H. erectus*, though dental similarities to Meganthropus I and II were noted. The authors concluded their study by proposing a four grade model of hominisation, with *H. habilis* divided between the second grade (which included Bed I

H. habilis and Meganthropus) and the third grade (including Bed II *H. habilis*, Telanthropus, Sangiran B and Pithecanthropus IV). In a separate publication, Koenigswald expressed a desire to divide early (i.e. pre-*erectus*) *Homo* into subgeneric groups, and he emphasised both the large time intervals and the size difference between Bed I and Bed II *H. habilis* specimens (Koenigswald, 1964).

Meanwhile, other anthropologists, who for the most part were willing to accept L.S.B. Leakey *et al.*'s (1964) revised definition of *Homo*, had challenged the taxonomic validity of *H. habilis*. Oakley and Campbell (1964) pointed out that if the *Telanthropus capensis* type specimen (SK 15) were to be included in the new taxon, its specific nomen *capensis* would have priority over the nomen *habilis*. However, Oakley and Campbell recognised that within *Homo* the trivial name *capensis* was already occupied by the Boskop cranium, so *capensis* would only be a valid nomen for the new species if the species were to be referred to a genus other than *Homo*. Campbell (1964) nevertheless repeated his criticism of the nomenclature, and raised two further objections - firstly, that in a single lineage model there was insufficient 'morphological space' between *Australopithecus* and *H. erectus* to accomodate a new species, and secondly that it was arguable whether the new species should be referred to *Homo* rather than to *Australopithecus*.

Le Gros Clark (1964a) also gave a number of reasons why the material assigned to *H. habilis* should be considered australopithecine. One of these reasons was an *ad hominem* irrelevancy - that two of L.S.B. Leakey's earlier creations, *Zinjanthropus* and *Kenyapithecus*, had been relegated to the position of being junior synonyms of valid genera. Le Gros Clark's main arguments were:

a. The fossils were recovered from australopithecine deposits.
b. The estimate of cranial capacity for OH 7 was unreliable, and fell within the probable range of australopithecine capacities, and was in any case far below values characteristic of *Homo*.
c. The curvature of the OH 7 parietals owed more to the specimen's immaturity than to any affinity with *Homo*.
d. Features of the *H. habilis* frontal (strongly developed supraorbital ridges, pronounced post-orbital constriction) were australopithecine characters.
e. The size and shape of the *H. habilis* dentition did not warrant taxonomic distinction from australopithecine taxa.
f. The morphology of the OH 7 hand bones was also seen in an australopithecine metacarpal from Swartkrans, and the morphology of the OH 8 foot bones could be found in the Kromdraai talus and in a tibia and fibula from the Olduvai *Zinjanthropus* site.
g. The stone tools found in association with the fossils were not evidence for the presence of *Homo*, since tools might also have been made by australopithecines.

This latter point concerning the stone tools was argued more fully by Oakley (1964), who suggested that even if it were established that one group of hominids made stone tools while another group did not, this would at best be evidence for separation at the specific or subspecific level, rather than at the generic level.

Tobias (1964b) and L.S.B. Leakey (1964) published brief rejoinders to the criticisms of Campbell (1964) and Le Gros Clark (1964a): Tobias dealt with the nomenclatural issues, while L.S.B. Leakey answered some of Le Gros Clark's points concerning the morphological affinities of *H. habilis*. L.S.B. Leakey argued, by analogy with fossil equidae and suidae, that coexistent branches among the hominidae were to be expected, and he suggested that the metacarpal from Swartkrans and the tibia and fibula from the *Zinjanthropus* site at Olduvai (cited by Le Gros Clark as australopithecine postcrania indistinguishable from those attributed to *H. habilis*) might in fact be referrable to *Homo*.

Robinson (1965) contributed to the critical appraisal of *H. habilis* by challenging both the nomenclatural and morphological aspects of the new species. Robinson obtained measurements of the OH 7 dentition that differed from the values published in L.S.B. Leakey (1961b): Robinson compared his own measurements of OH 7 with sample ranges for *Australopithecus africanus*, *Australopithecus robustus* and *H. erectus*. He demonstrated that the shape index (L/B) for the OH 7 P_3 was outside the range of *A. africanus* and *H. erectus*, that for M_1 the shape index was outside the range of all three species and that for M_2 the index fell outside the range of *A. africanus*. Robinson, however, cast doubt on the 'phyletic valence' of the shape index, for its range of variation had not been established in *Homo habilis* and because it lacked the ability to discriminate between the non-habiline hominid taxa (whose ranges overlapped). Robinson also expressed misgivings about the cranial capacity estimate for OH 7, and commented on the chronological and morphological hiatus between

Bed I and Bed II specimens. In particular, he claimed that the OH 7 mandible had an australopithecine-like internal contour (with the corpus breath in the premolar region exceeding the inter-corpus distance), while OH 13 had the U-shaped contour and thin corpus characteristic of later *Homo*. A dimorphic pattern of australopithecine and hominine affinities was, he claimed, also observable in the respective specimens' dentition.

Robinson noted, however, that consideration of the Bed I and Bed II samples as separate species would create a problem in explaining how these species could remain in sympatry while possessing an essentially similar level of stone tool technology. Robinson's solution was to regard the Bed I and Bed II groups as chronospecies - that is, representatives of the same lineage sampled at different time horizons. However, one implication of this scenario, that morphological progression had been accompanied by virtual cultural stasis, was not explored by Robinson. Taxonomically, since the affinities of the *H. habilis* fossils were with *A. africanus* on the one hand and, via *Telanthropus*, with *H. erectus* on the other, the logical conclusion, according to Robinson, was to transfer *A. africanus* material to *Homo*, and for *Homo* to be revised to contain just two species, *H. transvalensis* and *H. sapiens*. The trivial nomen *transvalensis* was proposed in place of the more senior nomen *africanus* because, at that time, Robinson believed that the nomen *africanus* was already validly occupied within *Homo*.

Pilbeam and Simons (1965) raised a very similar set of criticisms to those expressed by Robinson (1965), and agreed that if the morphologically distinct Bed I and Bed II specimens sampled one species, this should be included with *Telanthropus* and *A. africanus* under the binomial *A. africanus*. Pilbeam and Simons justified their 'lumping' strategy by providing ecological arguments for the presence of polytypy in early hominid species: thus *A. africanus* and *H. habilis* were to be regarded as geographically isolated populations of the same species. Other anthropologists, for example Montagu (1965), preferred to maintain the generic distinction between *Australopithecus* and *Homo* but to include *Homo habilis* within *Homo erectus*.

2.1.3 Further discussion

Holloway (1965) supported the cranial capacity estimates for OH 7 given by Tobias (1964a), but expressed reservations about the creation of a new species. In a reply to Holloway, Tobias (1965a) compared the ranges of variation in cranial capacity of *Australopithecus* and extant great ape species and calculated that OH 7 had a cranial capacity at least 3 s.d. above the australopithecine mean. In the same year Tobias (1965b) published a review article in which he used both relative and absolute brain size estimates in further support of the morphological gap between *Australopithecus* and *H. erectus*. Tobias also expressed his preference for an evolutionary scenario in which 'gracile' australopithecines were ancestral to both *Homo* and to 'robust' australopithecines.

Tobias (1965c) confirmed his change of opinion (Tobias and

Koenigswald, 1964) of the affinities of OH 16, which he regarded as australopithecine. Nonetheless, he reaffirmed the morphological distinctiveness of the cranial remains of *H. habilis*, supporting his arguments with measurements of tooth crown breadths and areas, cranial capacity and mandibular size and robusticity, all of which were said to corroborate the generic distinction between the hominines from Bed I and Lower Bed II at Olduvai and the australopithecines from South and East Africa.

L.S.B. Leakey (1966) put forward an evolutionary scenario that differed from that of Tobias (1965b). L.S.B. Leakey noted that in certain characters (position of maximum cranial width, occipital morphology) the Lower Middle Bed II specimen OH 13 resembled *H. sapiens* rather than *H. erectus*, while the Basal Bed II hominid OH 16 resembled African and Asian specimens of *H. erectus*. L.S.B. Leakey suggested that there must have been two species of *Homo* evolving at Olduvai: one leading from OH 7, through OH 13, towards *H. sapiens*; the other from OH 16 towards an African variant of *H. erectus*. By the following year Tobias, too, was entertaining the possibility of polyphyletic evolution within *Homo*, posing the question "Dare we admit of side-branches of a cladistic element, in the Pleistocene phylogeny of modern man?" (Tobias, 1967, p. 46).

Meanwhile, the new species faced undiminished criticism. Bielicki (1966) largely reiterated Le Gros Clark's critique of the diagnosis of *H. habilis*, and further argued that *Australopithecus* and early *Homo* must have occupied the same ecological niche. Bielicki invoked the competitive exclusion principle (Gause, 1934; Hardin, 1960: that adaptively similar species are competitively excluded from the same niche) as implying that African fossil hominids must represent a single, evolving species. The debate between Robinson and Tobias continued in the pages of 'Nature', with arguments centred on the interpretation of comparative dental metrics and endocranial volumes (Tobias, 1966a; Robinson, 1966), and Tobias (1966b) and Holloway (1966) continued to disagree on the taxonomic implications of OH 7's large brain. Holloway argued that the range of variation of cranial capacity in Australopithecus had not been established with sufficient certainty to allow the exclusion of OH 7 from that genus, and he continued to hold this view at least until 1967 (Holloway, 1968). Robinson (1967) and Wolpoff (1969) also sought to show that the Olduvai type series could be subsumed within A. africanus without extending the range of metric variation in the latter taxon beyond that observed in some extant primate species. Pilbeam (1969) expressed reservations about drawing firm taxonomic conclusions from the apparently significant differences in cranial capacity between A. africanus and H. habilis, but he subsequently stated that OH 7 was specifically distinct from (though cogeneric with) A. africanus (Pilbeam, 1970).

A review article by Howell (1967) expressed support for the new taxon, and proposed that recently recovered dental remains from localities in the Lower Omo Basin should be referred to H. habilis, together with specimens from the Middle Breccia at Sterkfontein Extension Site. Howell (1968) and Coppens (1970; 1971) independently referred some dental specimens from Omo to H. habilis, but in later publications Howell attributed these specimens to A. cf. africanus

(Howell, 1969a) or A. africanus (Howell, 1969b). Holloway (1970a,b) switched his views and added his support for the new taxon, now stating that the difference in cranial capacity, together with other differences in cranial, dental and endocast morphology between Australopithecus and H. habilis warranted at least specific distinction.

Differences in opinion over the affinities of H. habilis also extended to the postcranial remains. Lisowski (1967) included the OH 8 specimen in his comparative ontogenetic study of the primate talus, and deduced that both H. habilis and Paranthropus (as represented by a talus from Kromdraai) resembled apes rather than modern humans in this aspect of their morphology. Day and Wood (1968) also compared the H. habilis and Paranthropus tali with those of modern hominoids, and suggested that while both fossil hominid specimens were morphologically intermediate between apes and humans, the hallux in the Kromdraai (Paranthropus) specimen retained the facility of partial adduction. Oxnard (1969) noted that the high degree of torsion in the H. habilis clavicle (OH 48) placed this specimen outside the range of modern man and within the 90% confidence limits of brachiating and semi-brachiating primates. Tuttle (1967) described pongid-like specialisations in the OH 7 hand, and suggested that the specimen might be attributable either to Paranthropus boisei or to another, unknown, hominoid species. Robinson (1972a) also suggested that OH 7 be referred to Paranthropus. Lewis (1973), in a comparative study of the wrist morphology of apes and humans, examined the damaged capitate from the OH 7 hand together with TM 1526, an intact capitate of A. africanus from Sterkfontein. He concluded that both fossil hominids retained primitive hominoid features that were incompatible with a human-like precision grip.

The OH 8 specimen was subjected to a number of biometric studies (Preuschoft, 1971; Archibald *et al*., 1972; Lewis, 1972; Oxnard, 1972, 1973; Lisowski *et al*., 1974, 1976; Wood, 1974). These studies achieved consensus, insofar as it was agreed the OH 8 talus resembled the only other known fossil hominid talus from Kromdraai. However, among extant primates and modern humans, different studies placed OH 8 closest to modern humans (Preuschoft, 1971; Archibald *et al*., 1972), African apes (Lewis, 1972) or the orang-utan (Oxnard, 1973; Lisowski *et al*., 1974, 1976). When another fossil hominid talus, whose morphology approximated that of the modern human talus, was discovered in the Upper Member of the Koobi Fora Formation, it became apparent that OH 8 might reasonably be attributed to the genus *Australopithecus* (Wood, 1974).

2.1.4 More material

For a number of years the hypodigm of *H. habilis* remained the holotype, paratypes and referred material of the original description, less, of course, OH 16 which had been formally withdrawn by Tobias (1965c). Although suggestions had been made in the original diagnosis that the *Telanthropus* material from Swartkrans, the Kanam mandible, the Chad cranial fragment and material from Ubeidiyah in Israel might belong in the new taxon, Tobias appeared reluctant to refer further material to *H. habilis*. The fossil hominid specimens from Ubeidiyah proved not to be diagnostic (Tobias, 1966c). After examining the Chad specimen Tobias regarded it as resembling *H. erectus* (Tobias, 1968), and he was equivocal about the affinities of Telanthropus, which resembled either *H. erectus* (Tobias, 1967) or *H. habilis* (Tobias, 1968). Fragmentary material from Omo was tentatively referred to *H. habilis* (Howell 1967, 1968) but the same material was subsequently retracted (Howell 1969a, 1969b). Brain (1967) reported two new mandibular fragments from Swartkrans (SK 1587, SK 1588) as belonging to a 'less robust hominid' than *Paranthropus*, but no taxonomic attribution was offered. Subsequently these specimens were referred to *Paranthropus* (Brain, 1970), although Brain recognised that 'the hominids probably extend the range of tooth dimensions for the Swartkrans *Paranthropus* sample' (Brain, 1970, p. 1114; his judgement was vindicated by the results of a subsequent morphometric study by Wood *et al.*, 1983). Two new hominid vertebrae from Swartkrans (SK 3981a and SK 3981b) were also referred to *Paranthropus*, largely on the basis of similarities to a Sterkfontein vertebra attributed to *A. africanus* (Robinson, 1970). Robinson regarded fossil *Homo* vertebrae as being more similar to those of modern *H. sapiens* than to *Paranthropus*, and an isolated vertebra from Swartkrans, SK 853, was referred to *H. erectus*, rather than to *Paranthropus*, on those grounds (Robinson, 1972b).

A reinterpretation of the affinities of other specimens from Swartkrans occurred when Clarke noticed that SK 847, a facial fragment classified as *Paranthropus*, was part of the same individual as SK 80, a palatal fragment attributed to *Telanthropus* (Clarke *et* al., 1970). The Telanthropus mandibles SK 15 and SK 45 were considered to match the new composite cranium structurally, and together the specimens were taken as clear evidence of the contemporaneity of Homo and Paranthropus at Swartkrans (Clarke and Howell, 1972). In both papers the authors took care not to assign SK 847 to any particular species of Homo, although they suggested that SK 847 and other Telanthropus specimens might "ultimately prove to be conspecific with OH 13" (Clarke and Howell, 1972, p. 333). Supporters of the 'single species' hypothesis opposed the attribution of any Telanthropus specimens (including the composite cranium) to Homo, preferring to regard them as small 'robust' australopithecines (Mann, 1970; Wolpoff, 1968, 1970, 1971a, 1971b).

Attention, meanwhile, was returning to East Africa, where artefacts and hominid remains had been recovered from early Pleistocene deposits at Koobi Fora in Kenya (R.E.F. Leakey, 1970) and a small Homo cranium had been found at the base of Bed I at Olduvai Gorge (M.D. Leakey, 1969; M.D. Leakey et al., 1971). The initial report of discoveries made at Koobi Fora in 1968 and 1969 suggested the presence of two forms of hominid: one of these, represented by ER 406, was apparently conspecific with A. boisei, but another cranium, ER 407, was thought to be either a 'gracile' australopithecine or, more probably, a representative of early (i.e. pre-erectus) Homo (R.E.F. Leakey, 1970). After further reconstruction of the specimen, and with the benefit of further hominid discoveries at Koobi Fora, it became clear that the affinities of ER 407 lay with the 'robust' australopithecines, and the specimen has since come to be regarded as a female A. boisei

(Clarke and Howell, 1972).

The new cranium from Olduvai Gorge, OH 24, was reported to possess a number of features diagnostic of *Homo* (M.D. Leakey *et al.*, 1971). While refraining from making a formal taxonomic referral, these authors noted a close resemblance between OH 24 and OH 13, a paratype of *H. habilis*. One of the criticisms of *H. habilis* had been that specimens such as OH 7 (Bed I) and OH 16 (basal Bed II) were morphologically distinct from stratigraphically younger material such as OH 13, suggesting that the species might contain material belonging to more than one taxon (Robinson, 1965). The discovery of OH 24 demonstrated that large and small specimens were contemporaneous. M.D. Leakey *et al*. (1971) offered sexual dimorphism as an explanation of the size variability in *H. habilis*, although they emphasised that taxonomic variation within the phenon group remained a strong possibility, incidentally echoing L.S.B. Leakey's (1966) hypothesis of polyphyletic evolution within *Homo*. The referral of OH 24 to *Homo* was challenged on the grounds that its cranial capacity was less than 600 cc. and that it had a 'dished' face, both of these features being australopithecine characters (Editorial, 1971). Tobias (1972) defended the specimen's attribution to *Homo* by quoting Holloway's new estimate of its cranial capacity (590 cc.) and by arguing that OH 24's facial 'dishing' was confined to the sagittal dimension, in contradistinction to the laterally-dished faces of the australopithecines.

Interest in the discoveries at Koobi Fora was heightened by the results of radiometric dating of samples of a tuff from the KBS artefact site which suggested an age of 2.6 Myr. for the hominid deposits (Fitch and Miller, 1970), although subsequent stratigraphic work showed that the 1968/1969 hominid remains came from the Upper Member, which overlay the KBS tuff. The 1970 field season at Koobi Fora yielded sixteen hominid specimens, all from the Upper (including Ileret) Member, of which three (ER 730, ER 731 and ER 737) were attributed to the genus *Homo* (R.E.F. Leakey, 1971). A further eleven specimens of *Homo* were recovered from the Upper Member in 1971, and on the basis of this enlarged sample Leakey suggested that the mandibular specimens ER 817, ER 820 and ER 992 resembled some of the *A. africanus* material from Sterkfontein (R.E.F. Leakey, 1972). However, rather than refer the Koobi Fora hominines to *A. africanus*, Leakey, perhaps influenced by the early radiometric date associated with the Koobi Fora fossils, proposed that the affinities between the two groups implied instead that the Sterkfontein collection sampled two lineages: *Australopithecus* and *Homo*. In commenting on R.E.F. Leakey (1972), Robinson (1972a) reiterated his view (Robinson, 1967) that the East African and South African gracile hominids should all be referred to the taxon *Homo africanus*.

Of the specimens recovered from Koobi Fora in 1972, sixteen were attributed to *Homo* (R.E.F. Leakey, 1973a): half of these specimens were known to have come from deposits overlain by the KBS tuff, and were thus thought to be older than 2.6 Myr. Four of the latter specimens (ER 1470, ER 1472,ER 1475 and ER 1481) were described in a separate paper (R.E.F. Leakey, 1973b) in which a brief taxonomic discussion concluded by attributing them to *Homo* sp. indet. This attribution was reaffirmed by Leakey in a paper which also suggested that the Homo mandibles from the Upper Member had affinities with H. habilis material from Bed II at Olduvai (R.E.F. Leakey, 1973c). Specimens attributed to Homo from the 1970-1972 collections at Koobi Fora were described in detail in papers in the 'American Journal of Physical Anthropology' (Day and Leakey, 1973; R.E.F. Leakey and Wood, 1973; Day and Leakey, 1974; R.E.F. Leakey and Wood, 1974; Day et al., 1975; Day et al., 1976).

More fossil hominid discoveries were made at Koobi Fora in 1973 (R.E.F. Leakey, 1974). These specimens were recovered from both Upper and Lower Members of the Koobi Fora Formation, and included two crania, ER 1805 and ER 1813. The 1973 hominid collection from Koobi Fora reinforced the view, first expressed tentatively in R.E.F. Leakey (1973a), that there was evidence for more than one 'gracile' hominid taxon in the early Pleistocene fossil record of East Africa. R.E.F. Leakey (1974) speculated that the overall sample of East African hominids might belong to four genera, consisting of (a) 'robust' australopithecines (b) 'gracile' australopithecines (including OH 24 and ER 1813) (c) Homo (including OH 7, ER 1470 and ER 1590) and (d) a primitive group including the mandible ER 1482. These genera were not, however, given names, and the 1973 collections from Koobi Fora were not referred either to new or to existing taxa. Furthermore, some palaeoanthropologists were reluctant to accept the ecological and evolutionary implications of multiple sympatric hominid lineages, as implied by Leakey's taxonomic scheme (Editorial, 1973, 1974).

2.1.5 Discoveries of the mid- and late 1970s.

A new hominid innominate from Swartkrans, SK 3155b, was described by Robinson (in Brain *et al*., 1974), and referred to the genus *Homo* . Robinson, who did not recognise the taxon *H. habilis*, discounted any affinities between SK 3155b and the 'robust' australopithecines and suggested that the specimen represented early *H. erectus*. This attribution was opposed by McHenry (1975a), who in turn emphasised the specimen's differences from OH 28, a hominid innominate referred to *H. erectus* by Day (1971). McHenry stressed SK 3155b's resemblance to australopithecine material, and suggested its attribution to a 'robust' taxon of that genus.

Preliminary reports of hominid discoveries at Hadar, Ethiopia, suggested the presence of two hominid taxa, one of which had 'affinities' to the robust australopithecines (Taieb *et al*., 1974). The 1974 season at Hadar produced further hominid remains of which four specimens (AL 199-1, AL 200-1, AL 266-1 and AL 277-1) were thought to indicate the presence of *Homo* at this site (Taieb *et al*., 1975; Johanson and Taieb, 1976). However, with the addition of a large quantity of fossils recovered during the 1975-1977 seasons, all the Hadar hominids were attributed to a single, new species of *Australopithecus*, *A. afarensis* (Johanson *et al*., 1978a, 1978b).

Fossil hominid remains from Laetoli were initially described as bearing a strong resemblance to specimens of *Homo* from other East African sites. The Laetoli sample exhibited primitive characters, but these, it was stated, were to be expected in the earliest members of the genus Homo (M.D. Leakey et al., 1976). The same primitive characters subsequently formed the basis of the diagnosis of A afarensis, and the Laetoli collection was incorporated in the hypodigm of that species (Johanson et al., 1978a; White, 1980).

A new fragmentary skull, Stw 53, was recovered from Member 5 at Sterkfontein (Editorial, 1976) and Hughes and Tobias (1977) enumerated several features distinguishing this specimen from known examples of Australopithecus (sensu lato). These included a lack of marked constriction in the temporal fossa, the disposition of the temporal lines, a thin protuberant brow, subnasal morphology, styloid process ossification, nature of the posterior margin of the lateral pterygoid plate, morphology of the mandibular ramus and fossa, and ramification of the upper molar roots. Overall the skull was said to bear strong affinities to H. habilis.

Boaz and Howell (1977) described a fragmentary cranium, Omo 894-1, from Unit G-28 of the Shungura Formation, Lower Omo Basin, Ethiopia. The authors emphasised the specimen's affinities to pre-erectus Homo material from Swartkrans, Olduvai and Koobi Fora, and to Javan material attributed to Homo modjokertensis, noting that the latter taxon might have nomenclatural priority over H. habilis.

Clarke (1977) reclassified a juvenile cranium (SK 27) and two upper premolars (SK 2635) from Swartkrans. Clarke placed these specimens in Homo, noting their resemblance to SK 847.

2.1.6 Taxonomic problems, phylogenetic implications

Evidence for the existence of *Homo* at 2.9 Myr. ago (R.E.F. Leakey, 1973b) had immediate implications for hominid systematics. The apparent early appearance of *Homo* in the fossil record, and the inferred long period of coexistence between *Homo* and *Australopithecus*, provided further arguments against the hitherto influential 'single species hypothesis'. Tobias (1973a) published a phylogeny for the hominids that showed *Homo* diverging from the lineage of *Australopithecus* more than 3 Myr ago, predating the diversification of *Australopithecus* into 'gracile' and 'robust' forms. Tobias' new phylogeny implied at least 2 Myr. of coexistence between the two genera, in contrast to his earlier phylogenies in which *A. africanus* and *H. habilis* shared a common ancestor in the Lower Pleistocene (Tobias, 1965b, 1967).

In reviewing all the hominid evidence, Tobias interpreted the multiplicity of synchronic forms as indicating that 'hominid evolution has been cladistic in character and not predominantly phyletic' (Tobias, 1973b, p. 311). The new early date for the appearance of *Homo* also formed the basis of suggestions that the *Homo* lineage might in fact be of greater antiquity than that of *Australopithecus* (R.E.F. Leakey, 1976a; 1976b), and Oxnard (1975) cited the evidence for an early divergence of *Homo* as supporting his functionally-based argument that no species of *Australopithecus* could be ancestral to *Homo*. By the late 1970s, however, radiometric, palaeomagnetic and biostratigraphic studies supported a date of less than 2 Myr for the Koobi Fora hominids, while improved dating of the

South African sites, together with the discoveries of early australopithecines at Hadar and Laetoli, led Tobias (at least) to revert to more a conventional phylogeny with *A. africanus* once more occupying the ancestral position (Hughes and Tobias, 1977; Tobias, 1978a, 1978b).

The large supply of new hominid material from East Africa did little to promote consensus among palaeoanthropologists on the taxonomy of *Homo*. In particular, *H. habilis* only gradually gained acceptance as a valid taxon. Brace *et al.* (1972) sought to demonstrate that, on the basis of absolute tooth size, the Olduvai type series could be distributed between *A. africanus* and *H. erectus*, ignoring the fact that the dental diagnosis of *H. habilis* largely resided in comparisons of tooth crown *shape* and *relative* tooth size. Read (1975) similarly disregarded these important aspects of the diagnosis when seeking to show that *H. habilis* was indistinguishable from a pooled sample of australopithecines. Wells (1973) accepted the distinctiveness of *H. habilis* from *A. africanus*, and was willing to include both OH 24 and ER 1470 in the same species as the Olduvai type series. However, he was reluctant to accept that *H. habilis* had achieved the same evolutionary grade as *H. erectus*, and preferred that *habilis* be referred either to *Australopithecus* or some other, unnamed hominid genus.

In a paper given at the Wenner-Gren Conference in 1974 Campbell argued that the boundaries of sequential taxa within a lineage should be determined chronologically rather than morphologically, and hence "*both anatomy and dating are necessary to create the taxonomy of* fossil lineages" (Campbell, 1978, p. 569; emphasis in the original). This statement, however, only referred to subgeneric taxonomic categories, for Campbell adhered to the convention that "a new genus name in a lineage or radiation should be coincident with a new adaptive plateau" (Campbell, 1978, p. 576; emphasis in the original). Campbell regarded H. habilis as being only subspecifically distinct from the South African hominids, all of which were grouped by him as one species, A. africanus. This combined species was referred to Australopithecus rather than to Homo on the grounds that the hominids inhabited biomes characteristic of the former genus (the 'savannah phase' of human evolution) rather than the 'unrestricted' range of biomes characteristic of Homo.

Groves and Mazak (1975), taking advantage of the uncertainty created by the wealth of new specimens from Koobi Fora, erected a new species, Homo ergaster, which incorporated many of the gracile hominids from the Upper Member of the Koobi Fora Formation (most of these specimens were informally attributed by other workers to H. erectus). Groves and Mazak limited the hypodigm of their new species to specimens from the Upper Member at Koobi Fora (Loxodonta africana and Metridiochoerus andrewsi zones) and thus excluded ER 1813, the specimen that was perhaps most deserving of taxonomic attention. At that time ER 1813 was thought to have come from Lower Member deposits, presumed to be of much earlier date than those of the Upper Member. Groves and Mazak failed to distinguish their new species from H. erectus, except in respect of the anterior dentition, in which Homo ergaster was said to possess "incisors and canines similar in size to Homo africanus (Dart, 1925) and H. habilis", and thus presumably unlike *H. erectus* (Groves and Mazak, 1975, p. 243). Since incisor size was one of the characters quoted in the original diagnosis of *H. habilis* as distinguishing *H. habilis* from *Australopithecus*, the value of this particular aspect of Groves and Mazak's diagnosis is questionable.

R.E.F. Leakey (1976b) viewed some of the specimens from East Africa, including the small cranium ER 1813, as possibly representing a northern deme of *A. africanus*, while holding that the larger specimen ER 1470 belonged to the same species as OH 7. However, Leakey did not favour the retention of the taxon *H. habilis*, preferring a scheme that placed all specimens of *Homo* in a series of grades of the two species *H. erectus* and *H. sapiens*. Wood (1976a) compared ER 1470 with both *H. habilis* and *H. erectus*, noting that the specimen differed from the former species but shared a few similarities with the latter. Walker (1976) clarified the distinction between gradistic and cladistic classifications, and stated his intention to "classify things on the basis of what they look like, rather than on what they might evolve into" (Walker, 1976, p. 485). Walker believed that the material from Koobi Fora could be attributed to genera, and provided guidelines for classifying specimens at that taxonomic level. Walker implied that the species *habilis* had been included in *Homo* on cladistic grounds, and it was notable that he excluded the hypodigm of *H. habilis* from the group of *Homo* specimens on which he based his generic diagnosis. In comparing ER 1470 with his restricted hypodigm of *Homo*, Walker was able to show that the specimen's features predominantly matched those found in *Australopithecus*.

Walker retained this view in a subsequent paper (Walker and Leakey, 1978), whereas Leakey preferred to accomodate ER 1470 within *Homo*. Both authors agreed, however, that there was evidence for three contemporary hominid species at Koobi Fora, both below and above the KBS tuff. In the Lower Member these species were (a) a 'robust' australopithecine, (b) a species comparable with *A. africanus*, and (c) *H. habilis*. In the Upper Member at Koobi Fora, the 'robust' and 'gracile' australopithecines survived, but *H. habilis* had been replaced, perhaps phyletically, by *H. erectus* (Walker and Leakey, 1978, p. 56).

Wood (1978a) discussed in some detail the taxonomic affinities of some of the more complete fossils from East African Pliocene to Early Pleistocene sites. Taking each site in turn, he grouped together individual fossils that seemed to be morphologically similar and then made metric comparisons between these groups. Wood contrasted the heterogeneity of the East African 'gracile' hominid remains with the relative 'conformity' of the remains from the same region that were attributed to *A. boisei*. He also raised, but did not resolve, the question of whether the species *H. habilis* was represented among hominid fossils at Koobi Fora. Wood further pointed out that the hominine fossils at Koobi Fora could not be placed easily in a single phylogenetic lineage leading to later *Homo*. He went on to suggest that ER 1813 might represent a lineage separate from that of ER 1470 and ER 1590.

Howell (1978), in a review of the African hominids, presented a revised hypodigm for H. habilis. He referred the postcranial specimens OH 8 and OH 35 to A. africanus and removed OH 6 (a paratype specimen) and OH 14 (referred specimen) from H. habilis. Howell furthermore included in H. habilis most of the 'gracile' hominids from the Lower Member at Koobi Fora, some additional material from Olduvai, four specimens from Swartkrans (including two former Telanthropus specimens, SK 45 and SK 847) and the fragmentary Omo cranium L.894-1.

Kennedy (1983) sought to demonstrate the existence of H. erectus in the Lower Member at Koobi Fora through the morphometric analysis of a femur, ER 1481a (a specimen referred by Howell, 1978, to H. habilis). Kennedy characterised this specimen as 'hyper-erectus', and discounted comparison with H. habilis on the grounds that the type series of the latter taxon did not include femoral material. Trinkaus (1984) replied that the characters that Kennedy (1983) proposed as being diagnostic of H. erectus were, in fact, widely distributed among both erectus and archaic sapiens populations, and that the early date of ER 1481a, together with its association with cranial remains referred to H. habilis, were suggestive of an affinity with the latter taxon.

Rose (1984), in a study of the hominid hip bone ER 3228, also suggested that H. erectus was present in sub-KBS deposits at Koobi Fora. He emphasised the similarities between ER 3228, OH 28 and Arago 44 and stated that attribution of ER 3228 to H. habilis would require a reappraisal of the affinities of other postcrania attributed to that species (Rose, 1984). Such a reappraisal had, in fact already been undertaken in Howell's revision of the hypodigm of H. habilis (Howell, 1978).

2.1.7 Cladistic analysis of early Homo

The first explicitly cladistic analysis of hominids was published by Eldredge and Tattersall (1975). These authors subsumed H. habilis within the taxon A. africanus, but in later cladistic reviews (Delson et al., 1977; Tattersall and Eldredge, 1977; Bonde, 1977; Corruccini and McHenry, 1980) H. habilis was treated as a distinct taxon. Delson et al. (1977) listed three synapomorphic character states linking H. habilis to H. erectus and H. sapiens: increased brain size relative to body size, increased height of maximum cranial width and a reduction in the size of the cheek teeth, with Homo-type (helicoidal) wear. Tattersall and Eldredge (1977) mentioned increased brain and body size and a Homo-like locomotor apparatus as establishing the Homo clade, while Corruccini and McHenry (1980) identified a number of dental synapomorphies linking H. habilis with later Homo. Olson (1978) offered a cladistic definition of the genus Homo, based on a hypodigm that included the australopithecine species A. africanus. Olson's taxon Homo africanus included both South African 'gracile' australopithecine hominids and East African specimens referred by other workers to H. habilis. In Olson's cladogram H. africanus appeared as the sister group of a clade containing H. erectus and H. sapiens, an arrangement which he retained in a later cladogram which included A. afarensis (Olson, 1981).

A number of studies of different regions of the skeleton yielded further possible synapomorphies linking early (i.e. pre-erectus) Homo specimens with later members of the genus: these synapomorphies included dental eruption sequence (Wallace, 1977, 1978); morphology of the maxillary dental arcade (Tobias, 1980a); the cranial base (Dean and Wood, 1981, 1982; Dean, 1986); endocranium (Saban, 1980; Falk, 1983); cranial vault and face (Olson, 1978; Wood and Chamberlain, 1986) and the size of internal cranial angles (Stringer, 1986).

The establishment of a sound, cladistic basis for the definition of the genus Homo allowed more rigorous taxonomic reviews of early Homo to be undertaken (Wood, 1985a; Stringer, 1986), whose results tended to confirm the view that H. habilis contains material attributable to more than one taxon. Wood (1985a) showed that both KNM-ER 1470 and KNM-ER 1813 were derived in the direction of later Homo, compared to the more primitive taxon A. africanus. However, according to Wood, consideration of the estimated cranial capacities of these two specimens precluded their belonging to the same species. Stringer (1986), accepting the arguments for placing KNM-ER 1470 and 1813 in separate taxa (Wood, 1985a), clustered other early Homo specimens around these two crania. One taxon, centred on KNM-ER 1813, was viewed as a small-bodied sister species to African H. erectus and H. sapiens. The other taxon, centred on KNM-ER 1470 and containing the type specimen of H. habilis, was seen as a more primitive species, that nonetheless possessed some of the masticatory specialisations of Australopithecus.

Lieberman (1986), in an independent analysis of the same material, also argued that the size variation in *H. habilis* was too large to accommodate within one species. Furthermore, some of the shape differences between the large and small size morphs were unlike the pattern of shape differences seen in extant dimorphic primate species. Lieberman suggested that the large and small forms represented separate sympatric species, designated *H. habilis* and *H.* sp. respectively. He also pointed out that there were biomechanical and, by inference, dietary differences between the two forms, but he was unable to determine which form was more closely related to later species of *Homo*.

2.1.8 Recent morphological studies of early *Homo*

Endocranium

Holloway (1976) reported some multivariate comparisons between hominid endocasts. His results showed that KNM-ER 1813 most closely resembled the South African 'gracile' australopithecines while KNM-ER 1470 fell between groups composed of 'robust' australopithecines and Indonesian *H. erectus* respectively. Further qualitative comparisons (Holloway, 1978) showed that the Olduvai *H. habilis* specimens OH 13, OH 16 and OH 24 exhibited few similarities with *A. africanus*, but that OH 16 matched KNM-ER 1470 closely in the frontal region, where both specimens showed *H. erectus*-like features.

Holloway (1980) made a new endocast for OH 7 and estimated the cranial capacity of the individual to fall in the range 700-750 ml. Wolpoff (1981) disputed Holloway's reconstruction; his own reconstruction giving estimates in the range 580-600 ml. However, Holloway (1983b), using the dimensions of Wolpoff's reconstruction of the OH 7 parietals, showed that reconstruction to be distorted and asymmetrical. Vaisnys *et al.* (1984) estimated the cranial capacity of OH 7 from linear measurements, using a multiple regression technique; this yielded a best estimate of 690 ml, which was very close to original estimates made for this specimen (Tobias, 1964a).

Saban (1980, 1982) described the middle meningeal vessel pattern in hominids, showing that in this characteristic the ER 1470 endocast resembled endocasts of *H. erectus* rather those of 'gracile' or 'robust' australopithecines. Falk (1983) claimed that while the frontal lobe of ER 1470 appeared 'completely human-like', ER 1805 possessed a fronto-orbital sulcus - a primitive hominoid character. Holloway (1986), however, stated that no fronto-orbital sulcus could be distinguished on this specimen. Falk and Conroy (1983), Kimbel (1984) and Falk (1986) documented the occurrence of the accessory (occipital-marginal) venous sinus system in hominoids, showing this system to be prevalent in *A. afarensis* and the 'robust' australopithecines, but absent in early *Homo* crania (including the disputed cranium ER 1805).

Face

Although Rak (1985) characterised the early *Homo* face as generalised (i.e. primitive), other authors have identified a number of apomorphic facial characters that link early *Homo* to later members of that genus. Olson (1978) listed the separation of nasion from glabella and the continuity of the fronto-nasal and fronto-maxillary sutures as synapomorphies of *Homo*, and cited these characters as supporting the allocation of the Swartkrans specimens SK 27, SK 47 and SK 847 to the genus. Kimbel *et al.* (1984) viewed the *H. habilis* face to be primitive in several respects, but characterised its superorbital torus morphology as being distinct from *Australopithecus* and resembling *H. erectus*. Stringer (1986) used transverse facial angles to document the wide variation in facial morphology among specimens attributed to *H. habilis*. While ER 1813 and SK 847 possessed the curved upper face characteristic of *H. sapiens* (ER 3733 and ER 3883 being more 'primitive' in this character), in the lower face, ER 1470, and to a lesser degree OH 24, exhibited some of the facial flattening found in the highly-derived robust australopithecines. Bilsborough and Wood (n.d.) also noted variation in early *Homo* in their multivariate phenetic study of the hominid face. Early *Homo* crania were closer to recent forms than were the crania of *Australopithecus*, but some specimens (including ER 1813) nonetheless clustered quite close to *A. africanus*. ER 1470 and SK 847 appeared in their analysis to be distinctly separate outliers: the former had nearest neighbours among *A. boisei*, while the latter was closest to ER 732 and other, small hominid crania. Wood and Chamberlain (1986), as a result of an overtly cladistic analysis, added reduced facial height and reduced subnasal prognathism to the list of facial characters defining *Homo*.

Basicranium

Dean and Wood (1982) analysed the morphological variation among 19 hominid basicrania, including nine specimens that had been attributed to pre-*erectus Homo*. *A. africanus* possessed a distinctly pongid-like base, in contrast to the more human-like cranial base of the 'robust' australopithecines and African *H. erectus*. OH 24, SK 847 and ER 1805 exhibited a combination of 'robust' australopithecine and *H. erectus*/ *H. sapiens* features, while ER 1470 and ER 1813 closely resembled the *H. erectus* crania (i.e. OH 9, ER 3733 and ER 3883). Kimbel *et al.* (1984) confirmed the *erectus*-like basicranial morphology of ER 1813, in respect of the position and angulation of its foramen magnum, but noted the *sapiens*-like angulation of its nuchal plane. Foramen magnum angulation (relative to the Frankfurt Horizontal) also emerged as a synapomorphy linking *H. habilis* with later *Homo* in the cladistic analysis of Wood and Chamberlain (1986).

Mandible

Mandibular material is represented in the type series of *H. habilis*, yet unassociated mandibles of early *Homo* continue to present taxonomic puzzles (Wood and Van Noten, 1986). Mandibular morphology received scant attention in the original diagnosis of *H. habilis*: the mandible was described as being smaller than in *Australopithecus* and lacking a bony chin (L.S.B. Leakey *et al.*, 1964). White *et al.*

(1981) compared H. habilis mandibles (OH 7, OH 13, ER 1483 and ER 1802) with those of A. afarensis and noted no difference in size or robusticity between the taxa, although H. habilis was said to possess a low lateral torus dividing the lateral hollow into superior and inferior parts. White et al. (1981) also described H. habilis mandibles as possessing a more vertical anterior symphyseal face with an incipient mental trigon, the posterior symphyseal region lacking well-defined transverse tori. In contradiction, Chamberlain and Wood (1985) found that while early Homo mandibles were similar in size to A. afarensis, they were on average distinctly more robust than the latter. It is notable that in Wood and Chamberlain's cladistic study of hominids no mandibular corpus (as opposed to dental) synapomorphies between H. habilis and later Homo were noted, although such synapomorphies were evident in other regions of the cranium.

Dentition

Dental characters figured largely in the original diagnosis of H. habilis. The taxon was described as possessing smaller molars than Australopithecus, bucco-lingually narrowed teeth, large canines relative to premolar size and absolutely larger incisors than both Australopithecus and H. erectus (L.S.B. Leakey et al., 1964). White et al. (1981) confirmed that a sample of early Homo teeth had bucco-lingually narrowed postcanine teeth, but in terms of size they appeared to be identical to those of A. afarensis. Stringer (1986) also confirmed bucco-lingual narrowing as a diagnostic character of H. habilis. Wood and Abbott (1983) established significant differences in the means, but extensive overlap in the distributions, of the lower molar crown areas of *H. habilis* and *A. africanus*. Wood and Abbott again found that *H. habilis* possessed a distinctively narrow M1, in this instance in comparison with three species of *Australopithecus*. Wood et al. (1983) showed that early *Homo* lower molars had relatively large mesial cusps compared to species of *Australopithecus* (a feature also reflected in differences in their primary crown fisure patterns), and that the coronal crown profiles of early *Homo* lower molars showed a more basally located point of greatest buccal projection.

Beynon and Wood (1986) examined enamel thickness and structure in naturally fractured hominid teeth. They divided their sample into three taxonomic categories: 'EAFROB' (*A. boisei*), 'EAFHOM' (early *Homo*, including *H. erectus*) and an unknown category. They found thicker enamel in *A. boisei* than in early *Homo*, even after correcting for inferred size differences between the two groups. *A. boisei* enamel also possessed narrower, steeper, less-curved Hunter-Schreger bands and less steep striae of Retzius. Differences were also apparent within the early *Homo* group: specimens conventionally attributed to *H. habilis* (OH 6, OH 16, ER 1802 and ER 1805) had thicker enamel (both raw and size-corrected data) and wider Hunter-Schreger bands than the specimens conventionally attributed to *H. erectus* (ER 820 and ER 3733).

Postcrania

Susman and Creel (1979) published a multivariate analysis of the OH 7 hand that revealed both ape-like and human-like characteristics. They adduced that the hand combined a strong grasping capability (a probable climbing adaptation) with an enhanced precision grip. This conclusion was reaffirmed in a quantitative study of the same material carried out by Susman and Stern (1979). Lewis (1981) included OH 8 in his study of the evolution of the human foot. Again, a combination of ape and human characteristics was noted, perhaps indicative of the retention of some grasping function in a role that was intermediate between arboreality and terrestriality. Susman and Stern (1982) in their analysis of the same material deduced that the OH 8 foot was a derived structure adapted for bipedalism, with little facility for abduction of the hallux, although when OH 8 was placed in articulation with the OH 35 lower leg the resulting talar-tibial joint exhibited enhanced dorsiflexion. A preliminary analysis of OH 62, a new H. habilis skeleton from Olduvai Gorge, suggests that this species is postcranially similar to A. afarensis (Johanson et al., 1987).

2.2 Comments on hominid morphometrics

2.2.1 Aims of morphometric description and analysis

Description of fossil forms

The description of hominid fossils has traditionally been carried out using a combination of qualitative and quantitative data. There are potential advantages in describing form in a quantitative fashion. Firstly, quantitative data are objective. Their accuracy can be determined by replicate measurement and they carry the same information to different observers (in particular, they are less influenced by language barriers). Secondly, quantitative measurement allows form to be described in an abbreviated or summary fashion. A lengthy verbal description of an object can sometimes be replaced by a set of measurements, with little or no loss of information. Thirdly, and perhaps most importantly, quantitative description provides the raw data for morphometric analysis and for the statistical testing of hypotheses concerning the fossils themselves and the species to which they belong.

Notwithstanding these apparent advantages, published descriptions of fossil hominids have only in part been based on quantitative data. Such descriptions have been largely qualitative, with quantitative data playing a subordinate role. Moreover, diagnoses of hominid species have without exception been phrased in qualitative terms (e.g. L.S.B. Leakey et al., 1964; Johanson et al., 1978a; Howell, 1978; Walker et al., 1986). There are practical reasons for the lack of emphasis on quantitative data in fossil description and species diagnoses. Standard measurement definitions are available for modern H. sapiens skeletal material (e.g. Martin, 1928; Howells, 1973) but there are problems in applying these standard measurements to some fossil hominid material. Fossils are often incomplete, distorted or in other ways poorly preserved. It is sometimes difficult to identify, on fossils, the homologous landmarks on which most standardised measurements depend, particularly when dealing with fossil species whose morphology is markedly different from that of modern humans. Some landmarks for standard measurements on modern human crania are present because of delayed suture fusion - such landmarks disappear in adults of other primate species.

Some of the main purposes of fossil description and species diagnosis can undoubtedly be achieved without recourse to measurement. For example, the provisional allocation of specimens to existing taxa and the identification of important diagnostic characters do not generally depend on the acquisition of measurements. The absence of any agreement on a standardised set of measurements applicable to all hominid species is a further severe limitation on the utility of quantitative data accompanying fossil descriptions. Fossils have been described and measured by a number of different workers using their own definitions and measurement techniques. Even where standard measurement definitions have been applied by different workers the results are often not comparable between studies (Howells, 1973). A further difficulty stems from the morphological complexity of hominid skeletal remains. Tobias (1980b) has referred to the 'morphology between the measuring points', implying that measurements can only sample aspects of the 'total morphological pattern' of a specimen, and might thus leave some significant aspects of morphology undescribed.

Taxonomic allocation and characterisation of species

Despite the above-mentioned difficulties, several workers have amassed their own comprehensive sets of fossil hominid measurement data, collected using standardised measurement criteria. Such data sets have allowed statistical techniques to be applied to the problem of taxonomic allocation of individual fossils (Kennedy, 1983; Wood and Abbott, 1983; Wood et al., 1983; Rose, 1984; Wood and Van Noten, 1986) and to the related problem of discriminating among fossil hominid species (Johanson and White, 1979; Tobias, 1980b; Bilsborough, 1984; Kimbel et al., 1984; Wood, 1985a; Stringer, 1986). Relevant to such studies are subsidiary questions concerning the amount of intraspecific variation in hominids, their degree of sexual dimporphism and the extent to which morphology may change within a lineage.

Sexual dimorphism figures largely in current interpretations of fossil hominid variablity. Qualitative estimates of degree of sexual dimorphism in hominids have been noted in systematic revisions (Howell, 1978) and in diagnoses of new species (Johanson et al., 1978a). Dimorphism has also been invoked to explain morphological variation among fossils at individual hominid sites, such as Arago (De Lumley and De Lumley, 1971), Koobi Fora (R.E.F. Leakey, 1971), Olduvai Gorge (M.D. Leakey et al., 1971) and Hadar (Johanson et al., 1978a). Quantitative assessments of the degree of sexual dimorphism in modern humans and living non-human primates are available (Hall (ed.), 1982; Wood, 1976b) and provide the basis for assessing degrees of dimorphism in fossil hominids (Wolpoff, 1976; Wood, 1985a, 1985b; Chamberlain and Wood, 1985; Frayer and Wolpoff, 1985).

Phylogenetic analysis

Phylogenetic schemes depicting the pattern of evolution among hominids have been proposed for over a century (Brace, 1981) but it is only in the last decade that such analyses have been based on quantitative data. Corruccini and McHenry (1980), Kimbel et al. (1984), Skelton et al. (1986), Wood and Chamberlain (1986) and Chamberlain and Wood (in press) have published cladistic studies of hominids based on quantitative data. All of those studies have either used quantitatively-defined discrete traits, or have converted continuous measurements into discrete traits for the purpose of cladistic analysis.

Study of evolutionary mode

Eldredge and Gould (1972) proposed that the predominant mode of evolutionary change was one of morphological stasis punctuated by short periods of rapid evolution. Since the appearance of their publication several authors have examined the hominid fossil record for evidence of stasis or of the opposite evolutionary mode of phyletic gradualism (Cronin et al., 1981; Rightmire, 1981; Wolpoff, 1984; Stringer, 1984; Rightmire, 1986; Hunt and Vitzthum, 1986; Turner, 1986). In some of these studies morphometric data has been used to quantify the amounts and rates of evolutionary change implied by phylogenetic hypotheses.

Analyses of functional morphology

Morphometric data have also been used to substantiate inferences about the biomechanical properties and functional roles of hominid skeletal remains. Such applications of measurement data have been largely confined to investigations of the postcranial skeleton. Morphometric data have been used to support functional interpretations of the hominid pelvis (Zuckerman et al., 1973), femur (Lovejoy, 1978), scapula (Vrba, 1979b), hand (Susman and Creel, 1979; Stern and Susman, 1983; Susman et al., 1984), knee (Tardieu, 1981) and mandible (White, 1977).

2.2.2 Methods of morphometric analysis

Information presented above supports the view that the main impetus for applying morphometric methods in hominid studies has been the desire to make quantitative comparisons between different specimens rather than to provide descriptions or interpretations of the specimens in isolation. Useful numerical comparisons between biological forms can be made using a small number of quantitative traits (Cherry et al., 1982) which together might only sample a few aspects of overall form. Even single variables, when appropriately quantified, may provide a basis for taxonomic inference, as seen for example in the discussion of the range of variation in hominid cranial capacity (Holloway, 1965; Tobias, 1965b) or in the analysis of hominid dental metrics (White, 1985; Hunt and Vitzthum, 1986). The majority of morphometric studies of hominids, however, have employed either bivariate or multivariate statistical methods.

Bivariate regression of logarithmically transformed variables is the basis of the method of allometry. This method interprets the scaling relationship between variables in terms of a model of differential growth. Pilbeam and Gould (1974) published the first allometric study of fossil hominids, and the technique has since been applied to hominid dental measurements (Wood, 1978b, 1979; Wood and Stack, 1980; Wolpoff, 1978, 1982; Hills et al., 1983; McHenry, 1984; Jungers and Grine, 1986), mandibular corpus dimensions (Wolpoff, 1977; Chamberlain and Wood, 1985), facial dimensions (Corruccini and Ciochon, 1979) and to hominid postcrania (Jungers, 1982; Wolpoff, 1983).

The first application of multivariate statistical analysis to data from fossil hominids was published by Bronowski and Long (1951), and since then over 40 such studies have been published (Table 2.01). All of these studies have utilised continuous linear or angular measurements, but they differ in their methods for removing the effects of size. In some studies efforts have been made to control for size through transformation of the data prior to undertaking the analysis. Hominids vary by at least two-fold in body size (McHenry, 1975b, 1984), and it is suggested here that morphometric comparisons

TABLE 2.01: Multivariate analyses of hominid morphometric data

Author(s) of study	Anatomical region	No. of variables	Transformation of data	Method of analysis
Bronowski & Long '51	Teeth	4	None	CVA
Ashton *et al.* '57	Teeth	7	Logarithms	CVA
Day '67	Toe phalanx	9	Angles & ratios	CVA, D^2
Patterson/Howells '67	Humerus	7	None	CVA
Day & Wood '68	Talus	8	Ratios	CVA, D^2
Boyce '69	Cranium	99	Normalisation	PCA
Howells '70	Cranium	70	None	CVA
Bilsborough '72	Cranium	105	None	CVA, D^2
Brace *et al.* '72	Teeth	8	None	CVA, D^2
Rightmire '72	Metacarpal	12	None	CVA
Bilsborough '73	Vault	16	None	CVA
Corruccini '73	Teeth	10	Normalise, Ratios to SSV	Various Distances
Robinson/Steudel '73	Teeth	12	Logarithms	CVA
McHenry '73	Humerus	18	Logarithms	CVA
Zuckerman *et al.* '73	Pelvis	9	Allom., Ratios to SSV	CVA, D^2 & Cluster
Corruccini '74	Vault	51	Ratios to SSV	D^2, PCd
Lisowski *et al.* '74	Talus	16	Logs, Ratios	CVA, D^2 & HDP
Stringer '74	Cranium	44	None	D^2
Corruccini '75b	Vault	12	Ratios to SSV	PCd
McHenry/Corruc. '75a	Pelvis	16	Allom., Ratios to SSV	PCd, PCA & Cluster
McHenry/Corruc. '75b	Humerus	16	Normalise, Allom., Ratios to SSV	PCd, PCA & Cluster
Corruccini '76	Cranium	13	Logarithms	Multivariate allometry

TABLE 2.01 [Contd.]

Author(s) of study	Region	Vbles.	Transformation	Analysis
Ciochon/Corrucini '76	Scapula	9	Allom., Ratios to SSV	CVA, D^2, PCd & Cluster
McHenry <u>et al.</u> '76	Ulna	14	Allom.,Ratios to SSV, Normalise	PCd, PCA & Cluster
McHenry/Corruccini'76	Femur	10	Allom., Ratios to SSV	CVA
Holloway '76	Endocranium	19	None	CVA
Corruccini '77b	Teeth	24	Ratios to SSV	PCd, CVA, D^2
McHenry/Corruccini'78	Pelvis	48	Equalise variance	PCA, CVA, D^2 & Cluster
Steudel '78	Pelvis	8	Allom.	CVA
Feldesman '79	Ulna	9	Logarithms, Ratios to SSV	CVA, D^2, HDP, & Cluster
Susman & Creel '79	Hand	6	Various	CVA, D^2
Clark '80	Cranium	8	None	CVA, D^2
Corruccini/McHenry'80	Teeth	41	Normalise, regress on SSV	CVA, D^2, PCA & Cluster
McHenry '83	Capitate	11	Normalise, subtract SSV, Renormalise	CVA
Kennedy '83	Femur	14	None	CVA, D^2
Wood <u>et al.</u> '83	Tooth crown cusp areas	5	None	PCA
" "	Tooth crown fissures	11	None	Procrustes, PCd
Bilsborough '84	Cranium	77	None	PCA,CVA,D^2,GPA
Brauer '84	Cranium	8	None	PCA
Kennedy '84	Femur	12	None	D^2
Read '84	Teeth	12	Ratios & Compound variables	PCA
Van Vark '84	Cranium	17	None	CVA, D^2
Brauer & Leakey '86	Vault	8	None	PCA

TABLE 2.01 [Contd.]

KEY

Allom.	Allometry correction (from logarithmic regression).
Cluster	Hierarchical cluster analysis
CVA	Canonical variates analysis (=multiple discriminant analysis)
D^2	Mahalanobis distance
GPA	Generalised Procrustes analysis
HDP	High-dimensional plots
PCA	Principal components analysis
PCd	Principal coordinates analysis
SSV	Standard size variable

between hominids may be influenced, or even dominated, by size effects.

Many of the studies listed in Table 2.01 have sought to establish the morphological affinities between individual hominid fossils and extant primate species. The method of choice for such comparisons has been Canonical Variates Analysis (=multiple discriminant analysis) together with its distance metric, Mahalanobis D^2 (Van Vark, 1970; Blackith and Reyment, 1971). An advantage of D^2 over other measures of morphometric distance is that, by taking account of covariance between variables, conventional statistical parameters such as standard deviation and confidence limits can be assigned to values of D^2 (Howells, 1984).

Another multivariate technique, cluster analysis, has been used to extract hierarchical patterns of similarity among fossil and extant groups. The studies by Zuckerman et al. (1973), McHenry and Corruccini (1975a, 1975b), Ciochon and Corruccini (1976), McHenry et al. (1976), Feldesman (1979) and Corruccini and McHenry (1980) provide examples of the application of cluster analysis in hominid studies. Other multivariate methods that may prove to be suitable for describing and comparing biological forms include Finite Element Analysis (Lewis et al., 1980; Skalak et al., 1982; Cheverud, 1982; Cheverud et al., 1983; Cheverud and Richtsmeier, 1986), Fourier Analysis (Lestrel, 1974; Lestrel et al., 1977; Johnson et al., 1985; Lestrel and Roche, 1986) and a variety of techniques for comparing outline curves (Sneath, 1967; Olshan et al., 1982; Siegel et al., 1982; Yasui, 1986). These techniques have not yet been applied extensively in hominid morphometrics.

2.2.3 Problems of conventional morphometric methods

One objective in undertaking morphometric comparisons between biological forms is to reproduce, in numerical fashion, the 'gestalt' approach by which humans are supposed to intuitively assess the similarities between whole organisms (Howells, 1984). Palaeontologists are unable to sample the whole animal, nonetheless the skeleton appears to provide an adequate basis for morphological comparisons and inferences based thereon (Albrecht, 1976; Cherry _et al._, 1982; D.S. Wood, 1983). The palaeontologist, however, is confronted by further problems that stem from the nature of the fossil record. The first of these problems arises from the process of attributing fossils to taxonomic groups. The outcome of any morphometric analysis may depend on how fossils are assigned to groups, and this is particularly the case in allometric and multivariate statistical studies. To illustrate, Wolpoff (1977) identified an allometric scaling relationship in the hominid mandibular corpus, based on an analysis that treated hominids as a single taxonomic group. When a similar data set was taxonomically subdivided, however, substantially different scaling relationships were identified among the different taxonomic subgroups (Chamberlain and Wood, 1985).

A second problem encountered by palaeontologists is the incompleteness, distortion and poor preservation of many fossil specimens, which limits the amount of useful morphometric data that can be obtained from them. Missing data presents particular difficulties for multivariate comparison. Missing data values may necessitate the deletion of cases or variables from an analysis and can compromise attempts to correct for size differences if surrogate measures of size or compound size variables are being employed. A further difficulty affecting morphometric analyses of fossils lies in the limited sample sizes available. Small samples reduce the accuracy of allometric techniques. They also lead to unreliable estimates of character covariance, thereby compromising Canonical variates analysis and the calculation of Mahalanobis distance.

For these reasons there is an incentive, when undertaking morphometric studies of fossil material, to develop methods that are robust to missing data and that are independent of prior knowledge of the taxonomic affinities of the specimens under study. A further note of caution must be registered in view of what may be an uncritical emphasis on covariance techniques (Table 2.01). For taxonomic purposes, the problem is not to eliminate all covariance, but to remove covariation that is attributable to overall size, or to functional correlation, while retaining covariation that signifies taxonomic affinity.

2.3 Comments on hominid systematics

2.3.1 Species concepts in hominid palaeontology

As noted in the previous chapter, systematists of different schools agree that morphological discontinuity provides a way of identifying species in the fossil record. Hominid palaeontologists, however, have more often focussed on intraspecific variation rather than on between-species variation in their approach to species definition (Tattersall, 1986). Palaeontologists have sought to define palaeospecies that approximate living species in their degree of morphological variation. The palaeontologist's aim has been to identify morphologically homogeneous groups of specimens whose variability matches that of their closest relatives among living species (Wood, 1976a, 1978a; Martin, 1983). Where the variation in a sample of fossils exceeds that observed in closely related species, this is viewed as grounds for allocating the fossils to distinct taxa (Kay, 1982; Wu and Oxnard, 1983; Stringer, 1986).

Tattersall (1986) has pointed out that by concentrating their attention on within-species variation, palaeontologists will inevitably group together morphologically-similar though genetically distinct taxa (where such taxa are represented in the fossil record). Tattersall suggests that palaeontologists have underestimated the number of species in the hominid fossil record, and states that "where distinct morphs can readily be identified it would seem most productive to assume that they represent species unless there is compelling evidence to believe otherwise" (Tattersall, 1986, p. 168).

Tattersall (1986) favours the use of the cladistic definition of the species as a monophyletic group, defined by one or more uniquely derived characters (autapomorphies). Eldredge and Cracraft also advocate using autapomorphies to define palaeospecies, although they acknowledge that species can also be defined using plesiomorphic characters. Wood (1984) pointed out that a unique combination of primitive (plesiomorphic) and shared-derived (synapomorphic) characters can validly define a group and he applied such a definition in an analysis of the systematic position of H. erectus. A species that is defined using Wood's 'combination definition' is equivalent to Hennig's 'stem species' (cf. Bonde, 1981), which is directly ancestral to one or more descendant species or lineages. If the stem species only gives rise to a single descendant species or lineage it creates no problem for a cladistic classification, since the stem species and its descendant are sister groups and can be depicted as such on a cladogram. However, if the stem species has two or more direct descendants there will be an unresolved trichotomy on the cladogram. Some diagnoses of new hominid species, such as those defining H. habilis (L.S.B. Leakey et al., 1964) and A. afarensis (Johanson et al., 1978a) were, in effect, combination definitions sensu Wood (1984).

The central problem for any cladistic definition of a species is that it is relative, and not absolute. If the species is to be defined in terms of derived characters then the species definition is dependent on a character analysis. This, in turn, implies that the species is defined relative to a fixed phylogeny. To take species defined in such a way, and then to attempt to reconstruct their phylogeny using cladistic methods, would be illogical.

2.3.2 Evolutionary theory and hominid phylogeny

Brace (1981) has documented the succession of reconstructions of hominid phylogeny that have been offered since Haeckel (1899) and Schwalbe (1906) published the first phylogenetic trees depicting human evolutionary history. Some early trees, such as that of Haeckel (1899), were of necessity hypothetical, as the fossil forms were largely unknown or unrecognised at that time. The cumulative identification of species of fossil hominid, and the placement of these species in a stratigraphic sequence calibrated, in part, by absolute dating methods, have been the main incentive for subsequent revisions of hominid phylogeny. Hypotheses of hominid phylogeny have, however, been constrained by ecological and evolutionary theory, in particular by the concept of competitive ecological exclusion (Hardin, 1960) and by the notion that phyletic gradualism is the dominant evolutionary tempo (cf. Eldredge and Gould, 1972; Eldredge and Tattersall, 1975).

Competitive exclusion (Gause, 1934; Hardin, 1960) has been invoked to support the view that hominid evolution has been unilineal rather than cladistic in character (Mayr, 1950; Brace, 1967; Wolpoff, 1968, 1971b). Wolpoff (1968) argued that since the primary hominid adaptation was cultural, hominids would have been able to occupy an extremely broad ecological niche. Competition throughout this niche would have ensured that "no more than one culture-bearing hominid species could have arisen or have been maintained" (Wolpoff, 1968, p. 477). Conclusive demonstration of hominid coexistence at Koobi Fora, Kenya (R.E.F. Leakey and Walker, 1976), together with further evidence of Homo at the 'robust' australopithecine site of Swartkrans (Clarke, 1977), finally refuted this 'single species' hypothesis. Nonetheless, most of the hominid phylogenies published recently have admitted just one cladistic event in hominid evolution, namely that leading to the separation of the 'robust' australopithecine lineage (see Figure 5 in Skelton et al. (1986) for a list of phylogenies). Walker et al. (1986) have claimed that their recent discovery of an early, 'hyper-robust' skull at West Turkana refuted another unilineal hypothesis, namely that A. boisei evolved from A. africanus through A. robustus (Grine, 1981; Rak, 1983). Walker et al.'s discovery has prompted some anthropologists to add a further branch to their reconstructions of hominid phylogeny (Delson, 1986, 1987; Johanson, 1986) and these authors' response to the new evidence illustrates how the reconstruction of hominid phylogeny tends to be reactive to new fossil discoveries, rather than predictive of them.

The notion that 'phyletic gradualism' (gradual and directed morphological change within lineages) is the dominant evolutionary tempo has also constrained hypotheses of hominid phylogeny. Acceptance of phyletic gradualism implies that morphological boundaries between ancestral species and their immediate descendants are arbitrary (B.G. Campbell, 1978) and that a series of intermediate forms connect the species currently known from the fossil record (Cronin et al., 1981). Furthermore, it implies that a strong correlation exists between chronology and morphology and this has led some workers to place a great deal of importance on chronological data in phylogeny reconstruction. This point of view has been argued forcefully by Tobias: "Morphology without the time dimension may certainly be of some interest to the anatomist, but it has little to say of anthropological or evolutionary significance, and cannot contribute materially to any attempt to reconstruct the emergence and subsequent evolution of the Hominidae" (Tobias, 1980b, p.88). Phyletic gradualism is also integral to the method of phylogenetic reconstruction known as stratophenetics (Gingerich, 1977, Gingerich and Schoeninger, 1979; Gingerich, 1979) and Gingerich (1977, 1979) has advocated the application of stratophenetic methods to problems of hominid phylogeny.

2.3.3 Cladistic studies of the Hominidae

Cladistics is a method for determining sister-group relationships among taxa by examining the distribution of character states among those taxa. Advocates of the cladistic method have argued that a cladogram summarises all of the testable information contained in a phylogeny, and that hypotheses of ancestry are untestable (Eldredge and Tattersall, 1975; Delson *et al.*, 1977).

A cladistic perspective was introduced into hominid palaeontology when L.S.B. Leakey (1966) and Reed (1967) discussed the phylogenetic position of *H. habilis*, *H. erectus* and *H. sapiens*. However, nearly a decade passed before the first explicitly cladistic analysis of all the Hominidae was published by Eldredge and Tattersall (1975) (Figure 2.01). Eldredge and Tattersall followed the convention of representing phyletic relationships between taxa on a dichotomously branching tree, but they stated explicitly that they were unable to resolve a trifurcation at the morphotype of A. africanus, Homo and Paranthropus (the latter taxon including both A. boisei and A. robustus). The placement of A. africanus as the sister taxon of Paranthropus and Homo in their cladogram was justified by the 'primitive' or morphotypic nature of the former taxon, rather than by the presence of any shared derived characters in the latter two groups. H. habilis was incorporated in A. africanus for the purpose of their analysis.

Following discussions on hominid phylogeny at a conference held in 1975 (Bishop, ed., 1978), Bonde published cladograms depicting relationships among fossil hominids (Bonde, 1976, his Figure 5; simplified versions of the cladograms also appeared in Bonde, 1977, Fig. 5). Bonde's analyses were based on cranial, dental and pelvic characters. A simplified version of Bonde's 'best-fit' cladogram is reproduced in Figure 2.02. In common with Eldredge and Tattersall (1975), Bonde recognised that A. africanus was 'morphotypic' and hence its placement in the cladogram was uncertain, but he considered that the arrangement depicted here (Figure 2.02) was more probable than one in which A. africanus formed the sister group of Paranthropus and Homo.

Delson et al. (1977) attempted to resolve the trichotomy between A. africanus, Paranthropus and Homo by adding a consideration of postcranial morphology to Eldredge and Tattersall's earlier analysis. Their strategy was compromised by the rarity of clear associations

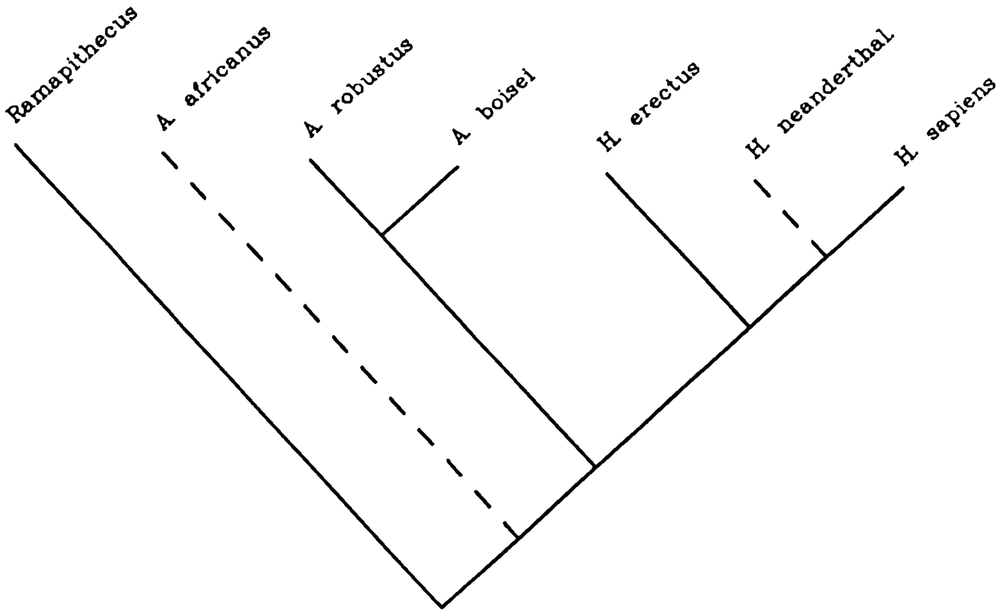


Figure 2.01 Cladogram from Eldredge & Tattersall (1975)

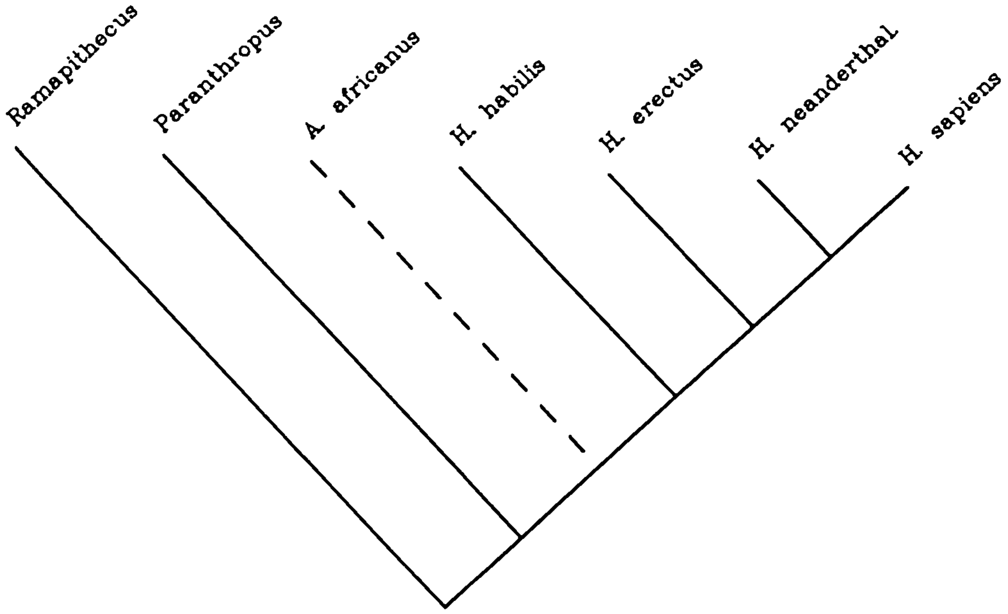


Figure 2.02 Cladogram simplified from Bonde (1976, 1977)

between cranial and postcranial elements in the hominid fossil record. However, Delson *et al.* (1977) found some grounds for inferring synapomorphies between *A. africanus* and *Homo*, in particular in their relative femoral and ischial lengths and in their degree of lumbar curvature. *H. habilis* was included as a distinct taxon in Delson *et al.*'s analysis, being placed as the sister taxon of later species of *Homo*. Their cladogram for the Hominidae was topologically identical to the 'best-fit' cladogram of Bonde (1977) (see Figure 2.02).

Tattersall and Eldredge (1977) published a cladogram that differed from their earlier analyses in linking *A. africanus*, *A. robustus* and *A. boisei* in a monophyletic group (i.e. an australopithecine clade). Their conclusion was based on a reinterpretation of the postcranial evidence considered by Delson *et al.* (1977), which led them to conclude that all australopithecines shared a locomotor complex that was derived relative to the primitive hominoid pattern retained by members of the genus *Homo*. Tattersall and Eldredge's cladogram, which was also published by Schwartz *et al.* (1978), is reproduced in Figure 2.03.

Olson (1978) defined the taxon *Homo africanus* in such a way that it included the fossil *Homo* material from Swartkrans and all material previously attributed to *A. africanus* and *H. habilis*. The two 'robust' species, *A. robustus* and *A. boisei*, were referred to the genus *Paranthropus*. The phyletic relationships between Olson's revised taxa were expressed on a cladogram that resembled, in its branching sequence, the cladograms of Bonde (1977) and Delson *et al.*

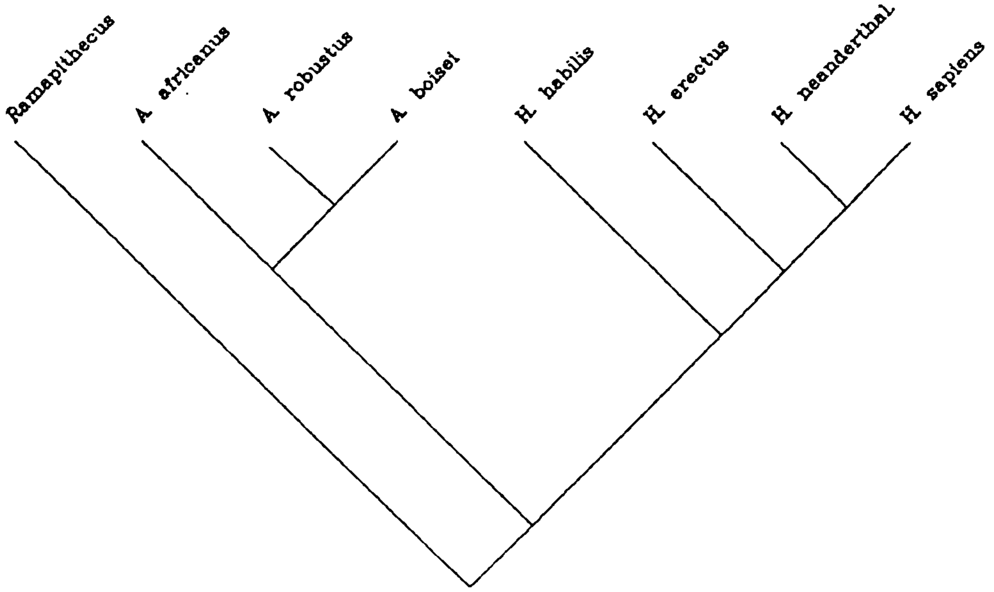


Figure 2.03 Cladogram from Tattersall & Eldredge (1977)

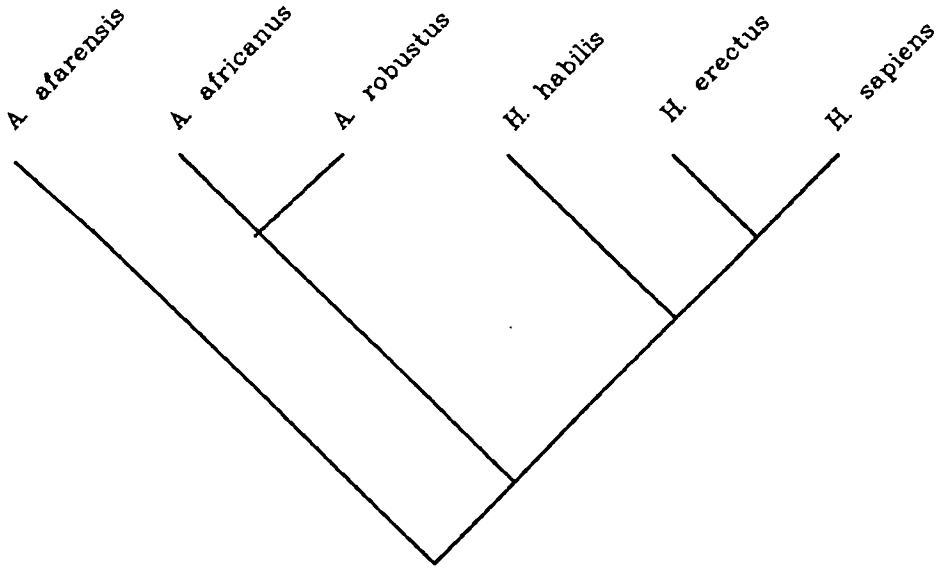


Figure 2.04 Cladogram from Johanson & White (1979)

(1977).

Johanson and White (1979) published a cladogram that differed from that of Tattersall and Eldredge (1977) on the following points only: *Ramapithecus* was removed from Hominidae and replaced by the new species *A. afarensis*, as the sister taxon of all other hominids, and the 'robust' australopithecines were included as a single species, *A. robustus* (Figure 2.04). In a later paper White *et al.* (1981) modified their cladogram (Figure 2.05), creating an australopithecine clade which was placed as the sister group of *Homo*. Both of their cladograms were accompanied by descriptions of derived characters of the face, mandible and dentition that were shared exclusively by *A. africanus* and *A. robustus*, but synapomorphies supporting the arrangement of the other hominid taxa were not given. The cladogram of White *et al.* (1981) was reproduced in Ciochon and Corruccini (eds.) (1983), with the appended comment that all hominid species, apart from *H. sapiens* and *A. robustus*, were morphotypic.

Corruccini and McHenry (1980) criticised earlier cladistic analyses of the Hominidae as lacking "clear definition of characters and demonstration of their morphoclinal variation" (Corruccini and McHenry, 1980, pp. 211-212). These authors based their own cladistic analysis of fossil hominids on 41 metrical characters, all but four of which were measured on the lower dentition. Polarity of morphoclines was determined by examining outgroups, and by considering ontogenetic change and functional morphology. Each character, after being standardised for size, was divided into discrete character states, with each character state corresponding to

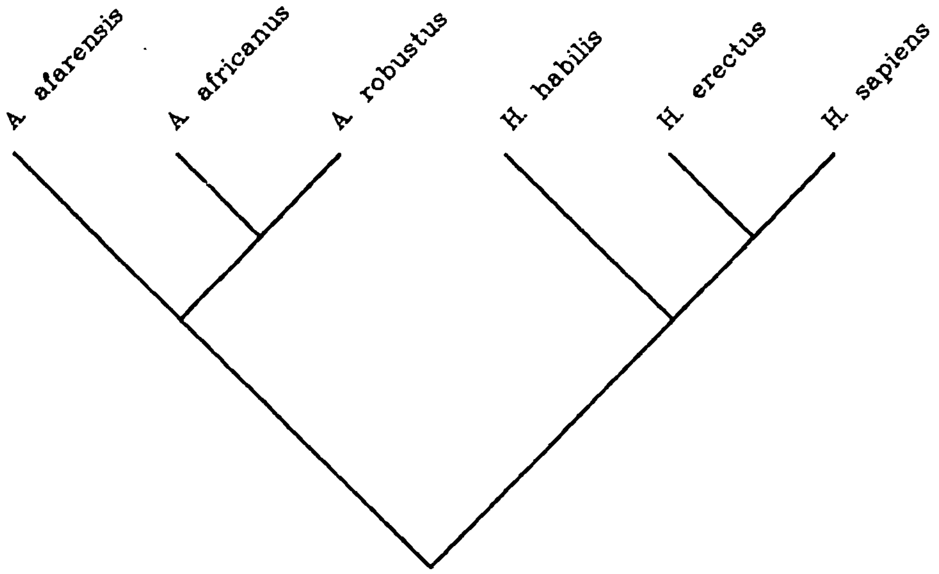


Figure 2.05 Cladogram from White et al. (1981)

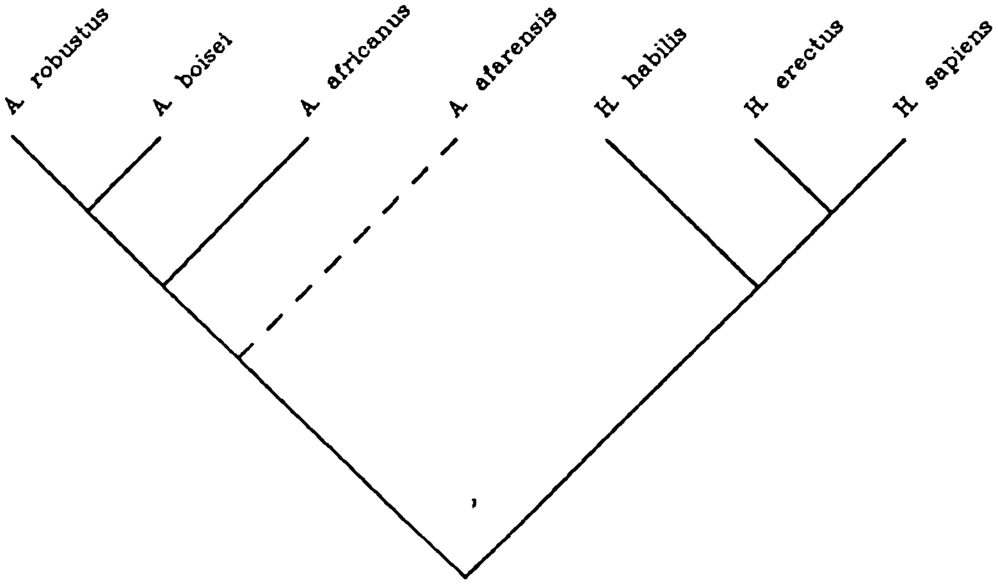


Figure 2.06 Cladogram from Corruccini & McHenry (1980)

a fixed proportion of the variance in the original linear measurements. The resulting cladogram (Figure 2.06) resembled the cladogram of White et al. (1981), but Corruccini and McHenry were unable to fully resolve a trichotomy between A. afarensis, Homo and a clade containing A. africanus and the 'robust' australopithecines. Corruccini and McHenry (1980) also indicated the distribution of character states on their cladogram, showing the high degree of homoplasy in their morphometric data.

Kimbel et al. (1984) also adopted a quantitative approach in their phylogenetic analysis of hominid cranial remains. These authors used measurements to support an extensive list of shared-derived characters in hominids. The cladogram based on the most parsimonious arrangement of their data is given in Figure 2.07, although the authors expressed a preference for a cladogram that placed A. africanus and the 'robust' australopithecines in a separate clade, as the sister group of A. afarensis and Homo. An alternative opinion of the phylogenetic affinities of A. afarensis was offered by Olson (1981). Olson rejected sexual dimorphism as an explanation for size variation in the hypodigm of A. afarensis, and proposed instead that the taxon be divided into a larger species (whose affinities lay with the 'robust' australopithecines) and a smaller species cladistically related to A. africanus and Homo. This cladistic hypothesis, which effectively distributed the hypodigm of A. afarensis across his earlier cladogram (Olson, 1978), was reiterated by Olson in a subsequent paper (Olson, 1985).

Wood and Chamberlain (1986) applied similar criteria to those adopted

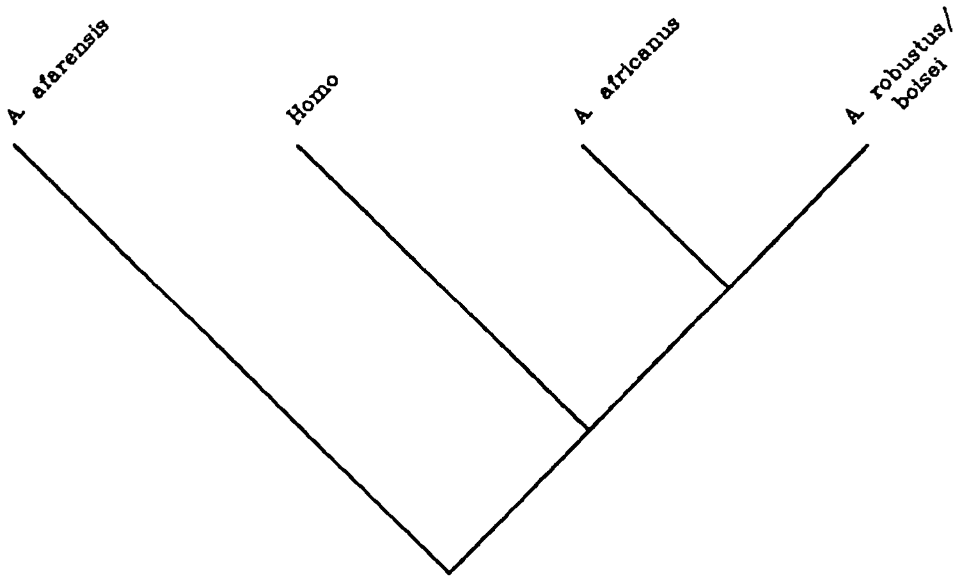


Figure 2.07 Cladogram based on data in Kimbel et al. (1984)

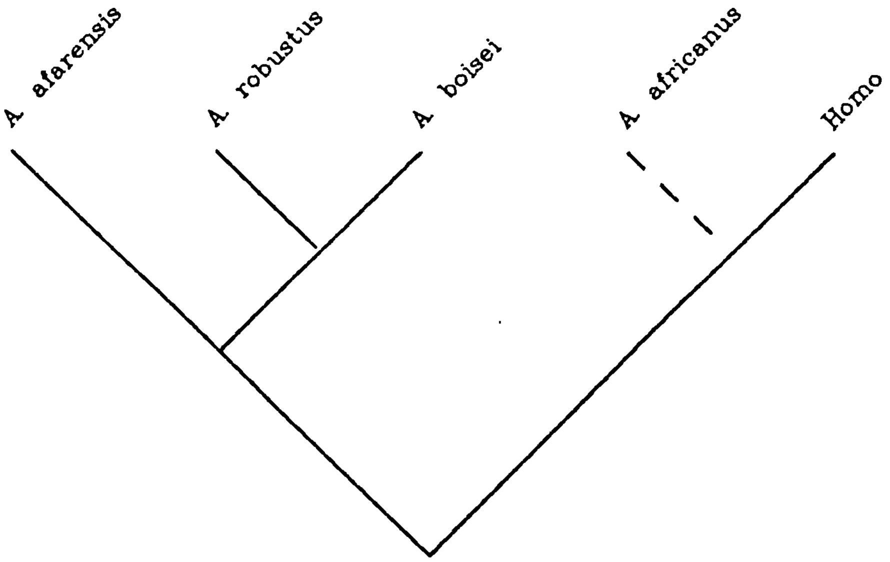


Figure 2.08 Cladogram of Wood & Chamberlain (1986)

by Corrucini and McHenry (1980) in compiling quantitative data for a cladistic analysis of cranial characters in *Australopithecus* and *Homo*. Wood and Chamberlain's data supported an arrangement of taxa in which *A. afarensis* shared a more recent common ancestor with *A. robustus* and *A. boisei* than with *Homo* (Figure 2.08). The position of *A. africanus* was uncertain, with little difference between a cladogram in which it was the sister group of *Homo*, and one in which it was the sister group of all other species of *Australopithecus*. However, both of these arrangements were more parsimonious than a cladogram in which *A. africanus* was the sister group of all other hominids, or of the 'robust' australopithecines.

Skelton *et al.* (1986) undertook a cladistic analysis of four hominid taxa (*A. afarensis*, *A. africanus*, *A. robustus/boisei* and *H. habilis*) using characters taken from the literature. Their 'best-fit' cladogram, supported by the distribution of 45 out of 69 characters, placed the 'robust' australopithecines as the sister group of *Homo* (Figure 2.09). Dean (1986) also provided evidence supporting a sister group relationship between *Paranthropus* (*A. robustus/boisei*) and *Homo*. Dean's analysis of characters of the cranial base and developing dentition did not include *A. afarensis*, but he was able to demonstrate that *Homo* and *Paranthopus* shared a number of derived characters of the regions considered. *A. africanus* retained primitive character states, similar to those found in great apes and other primates. Chamberlain and Wood (in press) carried out a further cladistic analysis of seven conventionally-defined hominid species, based on original measurements of 90 linear dimensions of the cranium and dentition (Figure 2.10).

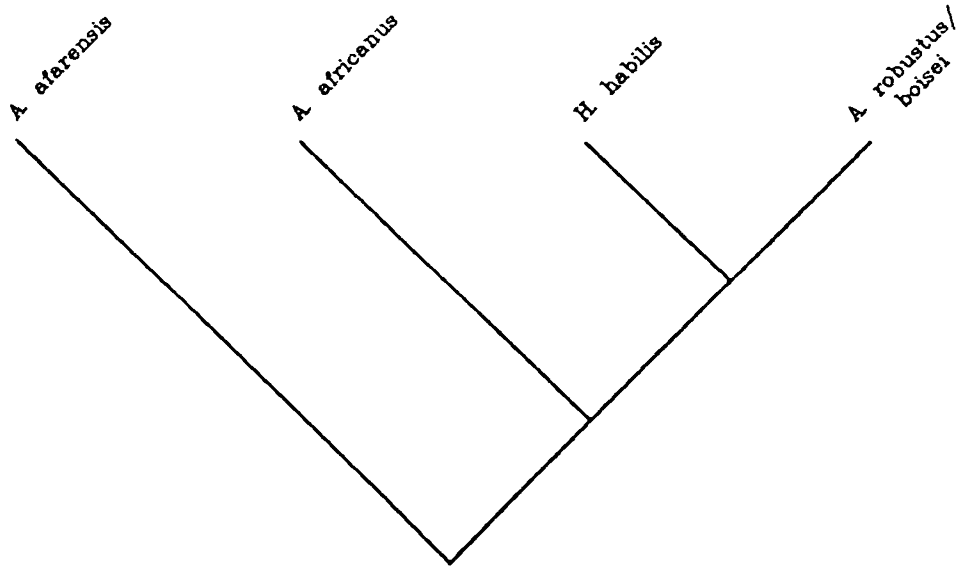


Figure 2.09 Best-fit cladogram of Skelton et al. (1986)

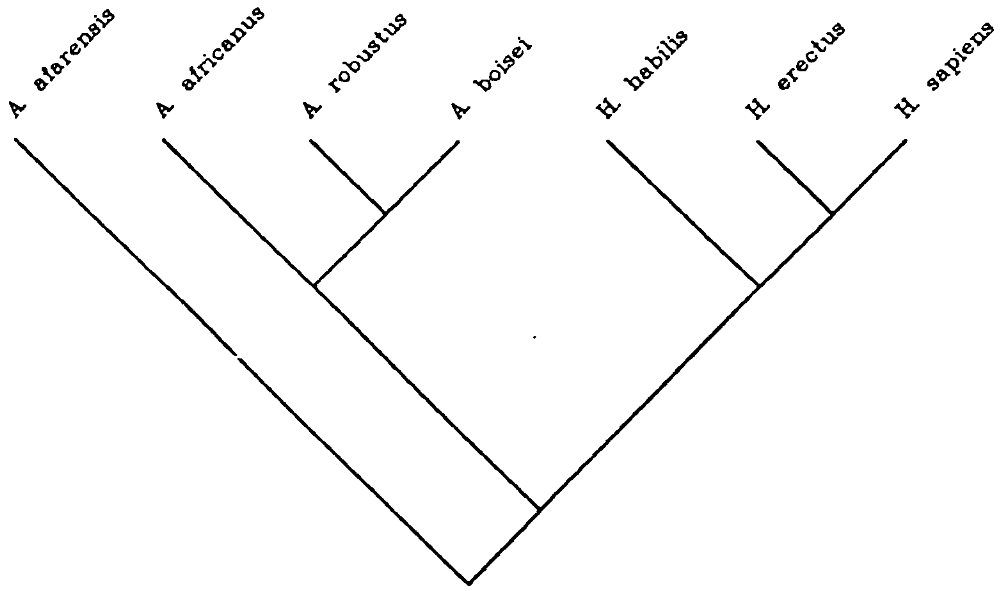


Figure 2.10 Best-fit cladogram of Chamberlain & Wood (in press)

CHAPTER 3: DATA COLLECTION AND METHODS OF ANALYSIS

3.1 Materials

3.2 Measurements

3.3 Methods of analysis

CHAPTER 3. DATA COLLECTION AND METHODS OF ANALYSIS

3.1 Materials

3.1.1 Fossil hominids

Hominid fossils and casts were measured during study visits to the British Museum (Natural History), London; Forschungsinstitut Senckenberg, Frankfurt; Geologisch-Paläontologisches Institut, Heidelberg; National Museums of Kenya, Nairobi and The Transvaal Museum, Johannesburg. Considerations of time, expense and availability of access to fossil collections precluded visits to institutions in Asia, Ethiopia, Tanzania and European countries apart from Britain and the Federal Republic of Germany.

The fossil hominids included in this analysis were chosen to represent all fossil hominid taxa except H. sapiens neanderthalensis. The analysis was confined to mandibles and crania for which a minimum of 10 measurements (mandibles) or 15 measurements (crania) could be obtained out of a standard list of 22 mandibular and 68 cranial measurements. An additional constraint on the selection of crania was that out of four regions of anatomical interest, in each specimen at least three of these regions should be represented by one, or more measurements. A total of 27 crania and 40 mandibles fulfilled these criteria and are listed in Table 3.01.

Most specimens were fully adult as judged by dental status and

TABLE 3.01

Hominid crania and mandibles included in the study

Specimen No.	Conventional Taxon	Number of Measurements	Location of Specimen (* indicates a cast)
--- CRANIA ---			
1. OH 5	*A. boisei*	64	NMK*
2. OH 9	African *H. erectus*	18	NMT#
3. OH 13	*H. habilis*	15	NMK
4. OH 24	*H. habilis*	32	NMK
5. ER 406	*A. boisei*	54	NMK
6. ER 732	*A. boisei*	21	NMK
7. ER 1470	'early'*Homo*	32	NMK
8. ER 1805	'early'*Homo*	39	NMK
9. ER 1813	'early'*Homo*	59	NMK
10. ER 3733	African *H. erectus*	56	NMK
11. ER 3883	African *H. erectus*	37	NMK
12. SK 46	*A robustus*	22	TM
13. SK 48	*A. robustus*	39	TM
14. SK 52	*A. robustus*	25	TM
15. SK 847	'early'*Homo*	30	TM
16. TM 1517	*A. robustus*	20	TM
17. Sts 5	*A. africanus*	58	TM
18. Sts 71	*A. africanus*	45	TM
19. StW 53	'early'*Homo*	25	WA
20. Ndutu	African *H. erectus*	17	NMK*
21. Bodo	Archaic *H. sapiens*	41	NMK*
22. Kabwe 1	Archaic *H. sapiens*	63	BM

TABLE 3.01 [Contd.]

Specimen No.	Conventional Taxon	Number of Measurements	Location of Specimen (* indicates a cast)
--- CRANIA ---			
23. Singa	Archaic H. sapiens	34	BM
24. Petralona	Archaic H. sapiens	53	BM*
25. Arago 47/21	Arch. H. sapiens	37	LA*
26. Sangiran 4	Asian H. erectus	38	FS
27. AL (composite)	A. afarensis	37	NMK*/BM*
--- MANDIBLES ---			
1. OH 7	H. habilis	12	NMK*
2. OH 13	H. habilis	20	NMK
3. OH 22	'early' Homo	16	NMK
4. ER 729	A. boisei	22	NMK
5. ER 730	'early' Homo	16	NMK
6. ER 818	A. boisei	13	NMK
7. ER 992	'early' Homo	19	NMK
8. ER 1482	A. boisei	16	NMK
9. ER 1802	'early' Homo	17	NMK
10. ER 1805	'early'Homo	10	NMK
11. ER 3230	A. boisei	21	NMK
12. ER 3734	'early' Homo	12	NMK
13. BK 67	'early' Homo	15	NMK
14. BK 8518	'early' Homo	19	NMK
15. Peninj	A. boisei	22	NMK*
16. SK 12	A. robustus	13	TM
17. SK 15	'early' Homo	17	TM

TABLE 3.01 [Contd.]

Specimen No.		Conventional Taxon	Number of Measurements	Location of Specimen (* indicates a cast)
--- MANDIBLES ---				
18.	SK 23	*A. robustus*	21	TM
19.	SK 34	*A. robustus*	19	TM
20.	TM 1517	*A. robustus*	15	TM
21.	Sts 7	*A. africanus*	15	TM
22.	Sts 36	*A. africanus*	16	TM
23.	Sts 52	*A. africanus*	22	TM
24.	MLD 18	*A. africanus*	18	WA
25.	MLD 40	*A. africanus*	16	WA
26.	LH 4	*A. afarensis*	20	KNM
27.	AL 128	*A. afarensis*	15	NMK*/BM*
28.	AL 198	*A. afarensis*	17	NMK*/BM*
29.	AL 266	*A. afarensis*	17	NMK*/BM*
30.	AL 277	*A. afarensis*	14	MK*/BM*
31.	AL 288	*A. afarensis*	18	NMK*/BM*
32.	AL 333	*A. afarensis*	16	NMK*/BM*
33.	AL 400	*A. afarensis*	21	NMK*/BM*
34.	Ckn. H1	*H. erectus*	12	LA*
35.	Ckn. K1	*H. erectus*	16	LA*
36.	Sangiran 1b	*H. erectus*	13	FS
37.	Sangiran 9	*H. erectus*	16	FS
38.	Arago 2	Archaic *H. sapiens*	16	LA*
39.	Arago 13	Archaic *H. sapiens*	16	LA*
40.	Mauer	Archaic *H. sapiens*	22	GIH

TABLE 3.01 [Contd.]

KEY TO LOCATIONS OF SPECIMENS

BM	Department of Palaeontology, British Museum (Natural History), London, England.
FS	Paleoanthropologische Abteilung des Forschungsinstitut Senckenberg, Frankfurt, Federal Republic of Germany.
GIH	Geologische-Paleontologische Institut der Universitat Heidelberg, Federal Republic of Germany.
LA	Department of Human Anatomy and Cell Biology, University of Liverpool, Liverpool, England.
NMK	National Museums of Kenya, Nairobi, Kenya.
NMT	National Museums of Tanzania, Dar-es-Salaam, Tanzania.
TM	The Transvaal Museum, Pretoria, Republic of South Africa.
WA	Department of Anatomy, University of the Witwatersrand, Johannesburg, Republic of South Africa.

The original of OH 9 was measured in the Zentrum der Morphologie, Dr. Senckenbergische Anatomie, Frankfurt, Federal Republic of Germany, by kind permission of Abel Nkini and Wolfgang Maier.

cranial suture fusion. The most notable exception was the OH 7 mandible, in which the third molars are unerupted (Day, 1986b). There was uneven representation by taxon, but all taxa were represented by at least one cranium and three mandibles (Table 3.02). Only three individual hominids (OH 13, ER 1805 and TM 1517) were represented by both cranial and mandibular specimens in this study. Crania and mandibles were considered separately in most of the analyses that follow.

In Table 3.01 the fossil hominids have been assigned to the conventional taxa *A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, 'early *Homo*', *H. habilis*, 'African' *H. erectus*, 'Asian' *H. erectus* and 'archaic' *H. sapiens*. In this Table, the category *H. habilis* is reserved for crania and mandibles from Bed I to Lower Middle Bed II at Olduvai Gorge (the type site for this species). The taxon 'early *Homo*' is used as a category for *Homo* crania that are distinct from *H. erectus* and *H. sapiens* but could belong to *H. habilis* or an unnamed species of *Homo*, and for *Homo* mandibles which are distinct from *H. sapiens* but could belong to *H. habilis*, *H. erectus* or an unnamed species of *Homo*. Thus in Table 3.01 there is a distinction between the crania of *H. habilis*, 'early *Homo* and 'African' *H. erectus*, but for the mandibles there is no *a priori* distinction between those of 'African' *H. erectus* those of and 'early *Homo*'. The sole exception to this is the mandible of ER 1805, which is associated with a cranium that excludes it from 'African' *H. erectus*.

The cranium of *A. afarensis* is represented in this study by a composite specimen reconstructed from measurements taken on the casts

TABLE 3.02

Number of specimens of each hominid taxon in the study

	Crania	Mandibles
'Archaic' Homo sapiens	5	3
Asian Homo erectus	1	4
African Homo erectus	4	- *
'Early'Homo/H. habilis	7	-
Australopithecus africanus	2	5
Australopithecus afarensis	1	8
Australopithecus robustus	4	4
Australopithecus boisei	3	5

* 11 mandibles belonging either to African H. erectus or to 'early'Homo/H. habilis were included in the study.

of three Hadar hominids: AL 200-1 (palate with full adult dentition), AL 333-1 (partial facial skeleton) and AL 333-45 (partial adult cranial vault and base). These specimens were the major elements of a reconstruction of a male *A. afarensis* cranium (Kimbel *et al.*, 1984). The justification for combining these separate specimens as if they represented the remains of a single individual is based on the arguments given by Kimbel *et al*. (1984), and by the similarity between palatal and dental measurements of elements common to both AL 200-1 and AL 333-1. Nonetheless, the results that depend on comparisons involving this reconstructed composite cranium must be treated as tentative.

3.1.2 Extant primates and modern humans

Ten adult male and ten adult female skulls were selected from collections of seven extant primate species. These species were *Colobus guereza*, *Gorilla gorilla*, *Homo sapiens*, *Hylobates lar*, *Pan troglodytes*, *Papio anubis* and *Pongo pygmaeus*. The skulls were measured at the National Museums of Kenya, Nairobi (*Colobus*, *Papio*), the British Museum (Natural History), London (*Gorilla*, *Hylobates*, *Pan*, *Pongo*), the Powell-Cotton Museum, Birchington, Kent (*Gorilla*, *Pan*), the Department of Human Anatomy and Cell Biology, University of Liverpool (*Gorilla*, *Pan*, *Pongo*), the Merseyside County Museums, Liverpool (*Gorilla*, *Pan*, *Pongo*) and the Department of Anatomy, University of the Witwatersrand, Johannesburg (*Homo sapiens*). The majority of the non-human primate skeletal material in the collections listed above had been obtained from animals living in the wild, but a few of the specimens in the British Museum (Natural History), and a large proportion of those in the Liverpool Anatomy collections, were obtained from captive animals. The catalogue numbers of the individual crania used in this study are given in Appendix 1.

In selecting male crania of *Pan*, *Pongo* and *Gorilla*, individuals with strongly-developed ectocranial crests were excluded. In the latter taxa, therefore, the male sample may not be representative of the species average. However, museum collections themselves are not random samples of the species which they represent. In particular, males of large than average body size, and parous females, may be over-represented in museum collections of large bodied primates. In this study the comparative specimens were also selected for completeness. Specimens with missing teeth, or with damage to areas from which measurements were to be taken, were largely excluded from the study, although for some taxa it was necessary to include a few specimens with missing data.

The sex of the specimens was determined from museum records, which in most instances relied on observations of soft tissue anatomy. The specimens' adult status was judged on the basis of their having completed dental eruption. The sample of modern *Homo sapiens* was selected from the dissecting room collection held in the Department of Anatomy, University of the Witwatersrand. Only individuals classified as 'black' under South African race legislation were included in this sample.

3.2 Measurements

3.2.1 Selection of measurements

Areas of anatomical interest

The measurements taken in this study were selected in order to sample different aspects of cranial, dental and mandibular morphology. In particular, those aspects of skeletal morphology that were known to vary among hominids, or to be diagnostic of a particular hominid, and that could be rendered unambiguously in quantitative fashion, were deemed suitable for inclusion. Lists of suitable measurements on the cranium and dentition are available (e.g. Howells, 1973; Tobias, 1980b) but these published lists can be biased towards particular anatomical regions or favoured aspects of morphology. To illustrate, in the extensive list of hominid morphometric variables given in Tobias (1980b) there is an over-representation of measurements of the cranial vault and of the dentition. In the present study, regions in which anatomical structures were functionally integrated were identified, after the manner of Bilsborough (1976). The mandible and lower dentition were considered as a single region, while the cranium was divided into four regions, the vault, base, face and the palate and upper dentition. A sample of measurements was defined within each region.

Selection of measurements

The primary intention in establishing regions was to ensure an even sampling of characters across the cranium. An additional constraint on the selection of measurements was the requirement that as far as possible measurements should be made between points located within a single anatomical region. This constraint was imposed in order to minimise the loss of information that inevitably occurs when fragmentary or poorly-reconstructed specimens are included in an analysis. For example, out of 19 measurements selected to characterise the face, only three were measured from porion (a point located on the calvarium). In this way, cranial specimens in which the anatomical relationships between the various parts of the cranium were poorly established could still be included in the study.

Originally, about twenty linear measurements and angles were defined within each region. The angular measurements were subsequently separated out, and were not used in the analyses that follow. The angular measurements were concentrated in the base and vault regions, and after these measurements were separated out the base and vault regions were depeleted in their numbers of measurements, compared to the face, mandible and palate regions (Appendix 2). Within each region an attempt was made to minimise the occurrence of direct functional correlation between characters. However, the list of measurements used in this study was based, in part, on a pilot study in which different analytical procedures were adopted (Wood and Chamberlain, 1986). As a result, a minority of the measurements used in the present study may exhibit a high degree of functional correlation. Measurements taken on the palate and upper dentition are highly correlated with similar measurements on the lower jaw and dentition. These regions were, however, treated separately in nearly all of the analyses that follow. The measurements of the dentition comprised the buccolingual and mesiodistal crown dimensions of the first incisors, canines, first premolars and the first and third molars. These teeth were chosen in order to sample changing function along the tooth row. Alveolar tooth row chords (viewed here as measurements of mandibular, rather than of dental morphology) were designed to overlap, but not to duplicate, the corresponding dental measurements. Thus the complete incisor, premolar and molar chords were measured, and the canine chord was omitted.

3.2.2 Definition of measurements

Within each anatomical region landmarks were defined (Appendix 2). The chosen landmarks were easy to identify and were, as far as possible, homologous between fossil hominids and a range of extant anthropoid primate taxa. The landmark definitions, and the secondary definitions of measurements that depend on them, were based on standard definitions found in several publications including De Villiers (1968), Howells (1973), Brothwell (1981), Dean and Wood (1981) and Wood and Chamberlain (1986). All measurement definitions used here are dependent on defined craniometric points and planes (Appendix 2). Many of the published definitions were modified as required for the purposes of the present study, either to simplify measurement techniques or to render definitions valid for all taxa considered in this study. This is not unusual in studies of this kind. Wood (1976b) also found it necessary to alter standard definitions in his comparative study of the primate skeleton.

Craniometric landmarks were given two-character symbols following a precedent established by Howells (1973) and Dean and Wood (1981). All measurements (except dental crown dimensions) have been defined as geometrical functions of landmarks and planes passing through defined points (Appendix 2).

3.2.3 Techniques of measurement

Most measurements were taken with commercially available equipment, comprising callipers (sliding, spreading and coordinate models), steel tape measure and goniometers. Angles in the sagittal plane and measurements of auricular height and posterior cranial length were made in the following way. A sheet of graph paper was fixed in a horizontal plane, and the cranium was positioned with its Frankfurt plane perpendicular to one axis of the graph paper and its sagittal plane horizontal. The relevant craniometric points were projected vertically onto the graph paper using a vertical spirit level.

Calliper measurements were recorded to the nearest 1 mm (for measurements greater than 50 mm) or to the nearest 0.5 mm (for some non-dental measurements under 50 mm, and for all dental measurements). Tape measurements were made to the nearest 1 mm, and goniometer readings were taken to the nearest 2° or 5°, depending on which device was used. Measurements of auricular height and posterior cranial length for the larger crania are probably only accurate to ± 2.5 mm, because of the measurement technique used.

Tooth crown measurements include a correction for interproximal wear. Two other types of estimated measurement used made in this study. Measurements between bilateral landmarks were occasionally estimated by doubling a measurement made from one side to the midline. This is indicated by the use of square brackets in Appendix 3. Another kind of estimate was employed when specimens were poorly reconstructed, or where the position of the relevant landmark could not be determined precisely. This is indicated in Appendix 3 by the use of round brackets, which are also used where dental crown measurements have been corrected for wear. Estimates were not used where the relevant skeletal part was missing, and I have generally taken fewer measurements on reconstructed specimens than have some other, more experienced (or more adventurous) physical anthropologists.

Measurements were recorded on data sheets, and were subsequently transcribed onto collated records prior to entering and storing the data on a microcomputer. Printouts of the computer files were visually checked against the original data sheets in order to eliminate errors of transcription.

3.3 Methods of analysis

3.3.1 A test of covariance matrix homogeneity

Cherry *et al*. (1982) proposed that measures of morphological distance that depend on pooled variance and/or covariance estimates may be unreliable when used to compare organisms that are taxonomically distant. This proposal was tested in the present study by comparing variance-covariance matrices (dispersion matrices) calculated separately for mixed-sex samples of *Pan* and *Pongo*, and by comparing dispersion matrices calculated for separate sex samples of *Pongo*. These primates were chosen because they model some of the differences seen between fossil hominid species, insofar as they differ (though not to a great extent) in size and shape, and because sexual dimorphism in *Pongo* is appreciable by comparison with other primate species.

N.A. Campbell (1978) noted that statistical tests of the homogeneity of dispersion matrices offer little help in determining whether such departures from the assumptions underlying multivariate methods are likely to lead to unreliable results. Nonetheless, in view of the suggestion that measures such as D^2 are sensitive to dispersion matrix inhomogeneity (Corruccini, 1975a; N.A. Campbell, 1978; Cherry *et al*., 1982), and in the absence of data pertaining to dispersion matrix inhomogeneity in interspecific analyses of primate skeletal measurements, it was considered a useful and prudent excercise to undertake such tests here.

Comparisons between group dispersion matrices were carried out using the discriminant procedure in the SPSSX package (SPSS Inc., 1986), which provides the test statistic 'Box's M'. In order to calculate this statistic the number of cases in the analysis must exceed the number of variables. The samples of Pan and Pongo comprised 20 crania of each taxon, and therefore five separate tests were carried out using up to 19 variables from each of the five cranial regions. Each test was duplicated on the same data following logarithmic transformation, because it is believed that such a transformation equalises differences in variance (Ashton et al., 1957).

The statistical significance of Box's M for each regional comparison is given in Table 3.03. The differences in dispersion between Pan and Pongo were statistically significant at $p < 0.05$ for all regions except the cranial base. Logarithmic transformation had only a marginal effect on reducing the statistical significance of these differences, which are presumably attributable to differences in covariance rather than variance (as might be expected considering the similarity in overall size between the taxa).

For the comparisons between the sexes within each of the taxa the smaller number of cases in each category (ten crania of each sex) necessitated testing dispersion matrices calculated from smaller numbers of variables. Since data for 90 variables had been collected a total of ten tests were carried out, each test being based on the data for nine variables. The statistical significance of these tests is given in Table 3.04. Only three tests gave a statistically significant difference within Pongo: two of these tests also proved

TABLE 3.03 Comparison of group covariance matrices between mixed sex groups of *Pan* and *Pongo*

Anatomical Region	Number of variables	SIGNIFICANCE OF DIFFERENCE BETWEEN GROUPS	
		Linear data	Log-transformed data
Base	16	0.06	0.14
Vault	13	0.01	0.02
Face	19	0.001	0.002
Palate	19	0.008	0.006
Mandible	19	<0.0001	0.0005

TABLE 3.04 Comparison of group covariance matrices for male and female samples of *Pan* and *Pongo*

Codes for Variables	Predominant Region	SIGNIFICANCE OF DIFFERENCE BETWEEN SEXES	
		Pongo	*Pan*
1 - 9	Base	0.08	0.30
10 - 18	Base	0.37	0.33
19 - 27	Vault	0.12	0.15
28 - 36	Face	0.13	0.10
37 - 45	Face	0.0005	0.02
46 - 54	Mandible	0.0002	<0.0001
55 - 63	Mandible	0.06	0.11
64 - 72	Lower dentition	0.05	0.82
73 - 81	Palate	0.004	0.90
82 - 90	Upper dentition	0.44	0.76

to be statistically significant for Pan. These significant differences in dispersion matrices appeared to be confined to aspects of cranial morphology (measures of facial prognathism, gnathic dimensions) that are particularly sexually dimorphic in extant primates.

It would appear from these results that dispersion matrix inhomogeneity is prevalent when comparisons are made between Pan and Pongo, but is largely absent from comparisons between the sexes within each of these taxa. These results endorse the use of covariance techniques in making interspecific comparisons, but must be seen as a qualification their use at higher taxonomic levels, if these results are representative of the usual pattern of between-taxon variation.

3.3.2 Size standardisation and the development of a shape function

Preamble

As an example of a qualitative statement of the kind encountered in sytematic studies, consider the statement that 'Tarsius possesses large eyes'. The reader would understand that the use of the expression 'large eyes' in this context is conditional, and that it is shorthand for 'large eyes for a primate of its body size'. The implied condition is important, because the absolute dimensions of Tarsius' eyes are small compared to those of human eyes, and are probably not even especially large by comparison with those of some small-bodied nocturnal animals. But for a small primate (the condition), Tarsius has rather large eyes.

I propose that if a morphometric method is to replace the kind of qualitative descriptions that prove useful in systematics, then it should take cognizance both of overall size and of the appropriate 'standard' against which even size-corrected data must be judged. Mathematically, this can be achieved by scaling a given form to a fixed overall size, and then measuring its deviation from a 'standard' form of the same size.

The choice of an appropriate standard is important: the standard should approximate the 'average' (or, more technically, the 'centroid') of the range of different forms that are to be compared. Use of a standard that is greatly dissimilar to all the forms under investigation would give an uninformative result, insofar as the deviations of all the forms from the standard would then be large, and in the same direction.

The 'common part removed' transformation

One way of comparing taxa while simultaneously discounting the effect of size difference is to use Q-mode linear regression or correlation (Sokal and Sneath, 1963). A recent example of this approach is the 'common part removed' transformation proposed by D.S. Wood (1983). In D.S. Wood's transformation a vector of measurements taken on a test specimen is linearly regressed against the same suite of measurements taken on a reference taxon. D.S. Wood (1983) referred to the variance accounted for by this regression as the 'common part', because it comprised the variance (in Q-mode) that was common to the test and the reference taxa. D.S. Wood considered the remaining, or residual variance to be of greater importance in taxonomic discrimination. He proposed that specimens of different taxa could be compared by regressing their measurements against the same reference taxon, subtracting the values predicted by each regression, and comparing the set of residuals generated for each specimen by this method. D.S. Wood (1983) supported this proposal by demonstrating the superiority of his method over conventional methods in an analysis of skeletal measurements of living avian taxa.

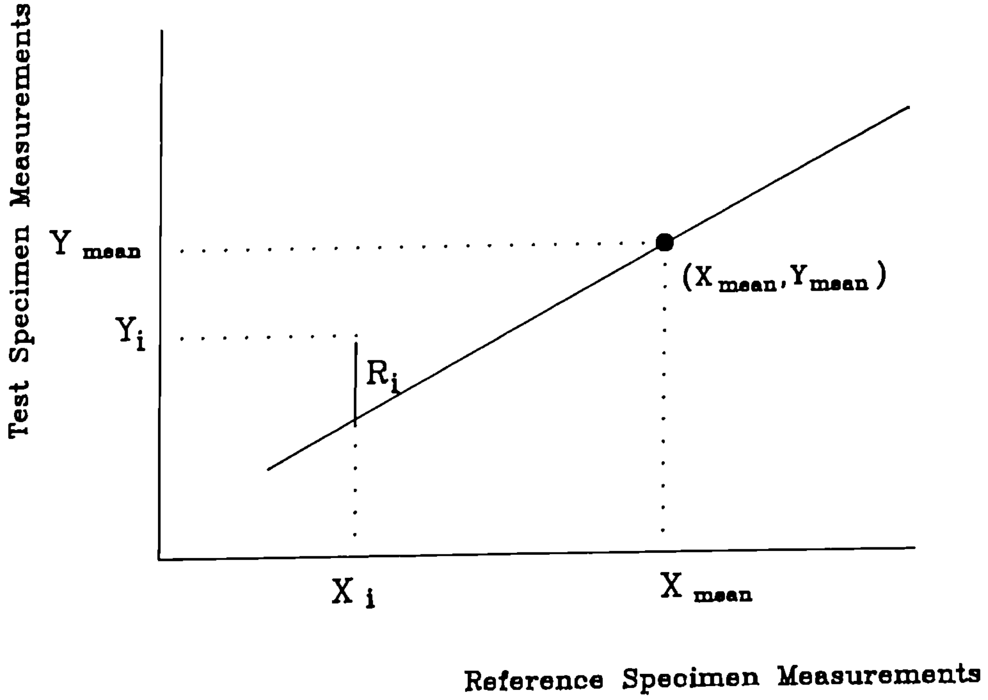
D.S. Wood (1983) did not explicitly state whether differences in size had an effect on morphological comparisons made using his method. It is easy to see, however, that Q-mode regression of measurements taken on objects of similar shape provides the basis of an effective size removal method. In a Q-mode regression the regression line will pass through the mean point (coordinates X_{mean}, Y_{mean} in Figure 3.01) and, for objects similar in shape, the line will also pass close to the origin. The line is constrained to pass near the origin because the average ratio between measurements of particular variables in the two taxa will be reasonably constant across the range of small to large measurements. The slope of the regression line will then approximate the average size ratio between the taxa, and the 'common part' that is subtracted comprises the measurements of the reference specimen scaled to the same size as the test specimen. The efficacy of size removal by a Q-mode technique will be demonstrated in a later section.

Q-mode regression of logarithmically transformed data

The method used in the present study differs substantially in detail from the method published by D.S. Wood (1983). Firstly, the set of reference measurements (the 'standard' against which specimens of other taxa are to be compared) was constructed by taking the average of several taxa, rather than by selecting a single specimen or taxon for use as the independent variate in the regressions. Secondly, all raw measurements were converted to logarithms as an initial step in the analysis. Thirdly, the slope of the regression line was fixed at unity, instead of being determined by a least-squares method. The rationale behind each modification to the original method is given below. I subsequently found that my adaptation of D.S. Wood's transformation is mathematically equivalent to a transformation used by Kazmierczak (Kazmierczak, 1985; Berge and Kazmierczak, 1986).

The purpose in taking a hypothetical 'average' primate as a reference specimen was to allow unbiased comparisons to be made between specimens of both 'outgroup' (extant non-human primate) and 'ingroup' (hominid) taxa. If a single non-human primate species had been used as the reference specimen the method might have led to less effective taxonomic discrimination among hominids than among other primates. The use of modern _Homo sapiens_ as a reference specimen might have led to the converse. By averaging the extant primate data (including modern _Homo sapiens_) the resultant reference specimen was morphologically equidistant (to a first approximation) from primates, fossil hominids and modern humans. The measurements of the reference

Figure 3.01 "Removal of the Common Part" (after D.S. Wood, 1983)



X_i = measurement 'i' on reference specimen

Y_i = measurement 'i' on test specimen

X_{mean} = Mean of reference specimen measurements

Y_{mean} = Mean of all test specimen measurements

R_i = Residual of measurement 'i' on test specimen

(Regression line is fitted by least–squares method) specimen (the 'average' primate) are given in Table 3.05.

The main reason for converting the original linear measurements to logarithms was to counter the non-normality of the data in Q-mode analysis. Biometric data is often normally distributed in R-mode, that is, linear measurements of a particular character tend to be normally distributed across a group of taxa, or across specimens within a given taxon. However, the distribution in Q-mode (i.e. the distribution of the magnitudes of different variables for a single taxon or specimen) is heavily dependent on the initial selection of variables. In the present study the measurement variables were selected prior to developing the analytical techniques, and I was not surprised to find that the reference measurements (average of all extant primates: Table 3.05) were strongly skewed in Q-mode (see Figure 3.02). Although the Q-mode distributions of raw measurements in individual extant species were not determined, it is likely that a marked degree of skewness was common to all of the taxa included in the study because of the kinds of measurements used. The list of measurements (Appendix 2) includes 20 dental crown dimensions which, in any primate taxon, will form a large proportion of the smallest measurements taken. This biases the Q-mode distribution towards the left, and the large dimensions (e.g. those of the cranial vault) provide a long tail to the right (Figure 3.02). Logarithmic transformation of the reference data set removed the skewness of the data (Figure 3.03) and though the resulting distribution exhibited significant negative kurtosis ($g_2 = -1.07$, $p < 0.05$) the distribution of the transformed data was regarded as suitable for regression analysis. Further transformations can be used to normalise a

TABLE 3.05

Reference measurements (from the 'average primate')

B1	92.7	V3	88.3	F8	12.9	M7	12.3	P3	28.2
B2	40.1	V4	95.5	F9	21.6	M8	19.3	P4	31.4
B3	22.2	V5	124	F10	76.0	M9	30.8	P5	7.99
B4	40.3	V6	72.7	F11	33.9	M10	11.2	P6	11.7
B5	60.6	V7	59.4	F12	44.8	M11	17.8	P7	14.0
B6	24.1	V8	58.5	F13	66.5	M12	33.9	P8	15.6
B7	27.6	V9	52.8	F14	25.5	M13	6.24	P9	14.5
B8	21.4	V10	80.6	F15	93.1	M14	6.87	P10	29.8
B9	18.9	V11	62.1	F16	129	M15	9.27	P11	9.68
B10	33.3	V12	63.8	F17	68.6	M16	10.2	P12	7.95
B11	26.0	V13	51.4	F18	9.88	M17	10.2	P13	11.1
B12	22.7	F1	88.8	F19	38.0	M18	8.48	P14	9.76
B13	44.2	F2	112	M1	39.5	M19	10.6	P15	7.72
B14	29.9	F3	82.4	M2	27.8	M20	9.21	P16	9.46
B15	62.0	F4	44.3	M3	26.3	M21	11.9	P17	10.3
B16	22.7	F5	81.9	M4	11.5	M22	9.99	P18	10.4
V1	3.40	F6	34.7	M5	12.4	P1	68.8	P19	10.1
V2	64.5	F7	15.5	M6	15.9	P2	52.8	P20	10.7

Measurements are in millimetres. Measurement definitions are given in Appendix 2.

platykurtic distribution (for example, the arcsine, or angular transformation, Sokal and Rohlf, 1981, p. 427) but this was not thought to be necessary in the present case.

The use of logarithmically transformed data also permitted a third modification to D.S. Wood's method, in that the slope of the regression line could be fixed at unity. As noted above, for two morphologically similar taxa the Q-mode linear regression line computed between raw measurements taken on specimens of each taxon will pass close to the origin. Under logarithmic transformation this line will be transformed to a straight line of approximately unit slope, intercepting the axis of the dependent variate at k, the log-transformed ratio between the averages of all measurements in each taxon (see below, and Figure 3.04).

Testing the assumption of average isometry with primate and hominid data

The assumption of unit slope is equivalent to an assumption that, on average, the measurements of any character on specimens of each of two taxa are related to each other by the same constant scaling factor. This assumption of average isometry between test specimen and reference specimen was tested by carrying out regressions of mean and individual data sets from three extant primate taxa (Gorilla, Pan and Homo sapiens) and individual data sets from four relatively complete fossil hominid specimens (two crania, ER 406 and ER 1813, and two mandibles, ER 729 and ER 992). The extant taxa were chosen in order to sample both dimorphic and non-dimorphic taxa, while the

Fig. 3.02 Q–mode Distribution (linear)

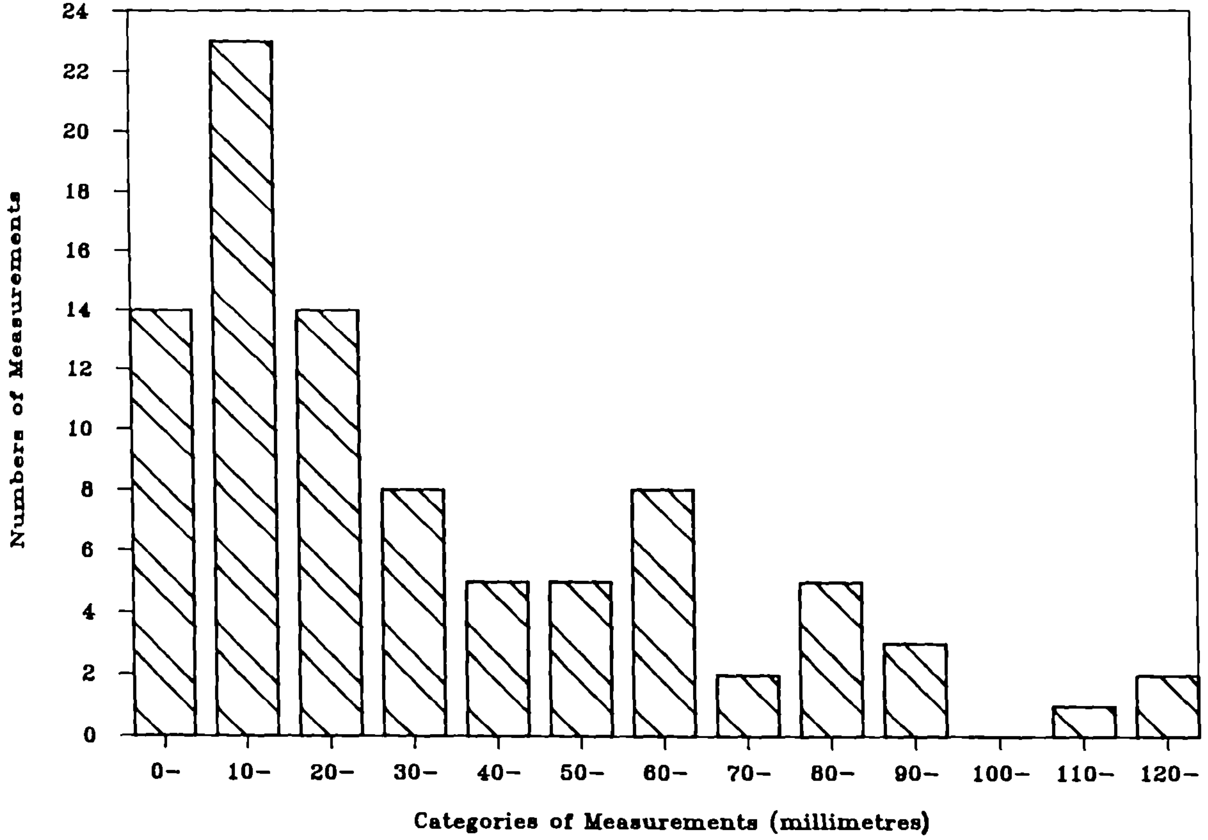
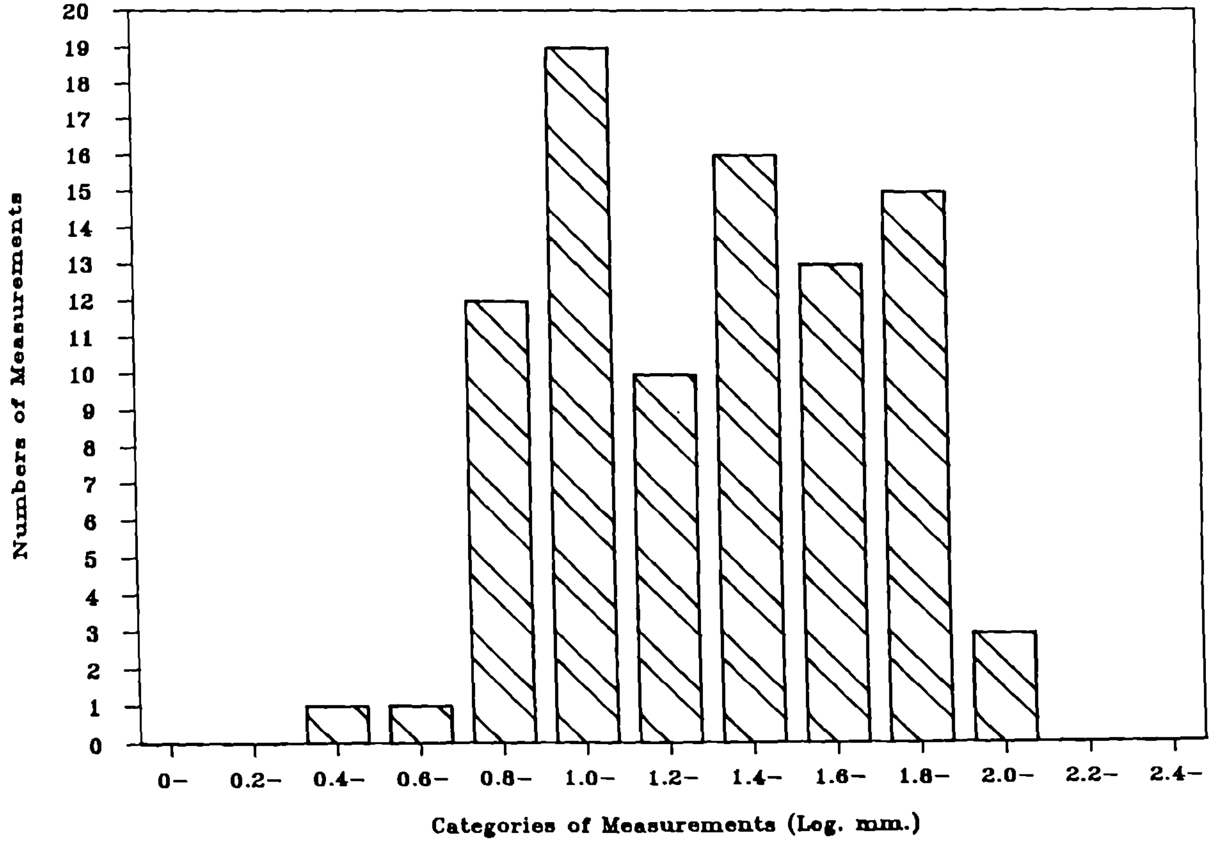


Fig. 3.03 Q–mode Distribution (logs.)



hominids were chosen to represent two morphologically contrasting (though contemporaneous) fossil hominid taxa; 'early' Homo and Australopithecus boisei.

As in most analyses reported here the crania and mandibles were treated separately. A total of 16 regressions were carried out and the results are given in Table 3.06. In all regressions the independent variate (horizontal axis) comprised the vector of log-transformed reference measurements (the measurements of the 'average primate'). The dependent variates in the regressions of Pan, Gorilla and Homo sapiens were (alternately) the set of log-transformed mean measurements for ten specimens of one sex, and (in separate regressions) the log-transformed measurements taken from a single individual of each of those species. Each of the four fossil hominid specimens was entered as an individual in separate regressions. In only one out of 16 regressions was there a significant departure from isometry at $p < 0.05$; such a result would be expected by chance in one out of 20 regressions of isometric data sets. Therefore this apparently isolated departure from isometry was not considered to be grounds for rejecting the assumption of Q-mode isometry between test taxa and the reference taxon.

The greatest departure from isometry, though one which was not statistically significant, was seen in the 'robust' australopithecine mandible ER 729. This specimen combines a relatively small anterior dentition with a relatively large mandibular corpus, compared to the mandible of the 'average' primate. Since the anterior dentition and the corpus provide, respectively, the smallest and largest dimensions

TABLE 3.06

Correlation coefficients and slopes of logarithmic Q-mode regressions of mean and individual specimen data sets against the measurements of the 'average primate'

	Cranial Measurements				Mandibular Measurements			
	r	b	se(b)	sd(res)	r	b	se(b)	sd(res)
Pan (female mean)	1.00	1.01	0.01	0.08	0.97	0.96	0.06	0.13
Pan (individual)	0.99	1.00	0.02	0.11	0.93	0.98	0.09	0.21
Gorilla (male mean)	0.99	0.98	0.02	0.12	0.98	0.97	0.05	0.11
Gorilla (individual)	0.99	0.99	0.02	0.07	0.99	0.90*	0.03	0.07
Homo (male mean)	0.96	1.07	0.04	0.26	0.96	1.09	0.07	0.17
Homo (individual)	0.96	1.05	0.04	0.27	0.95	1.06	0.07	0.17
ER 1813	0.96	1.01	0.04	0.26	-	-	-	-
ER 992	-	-	-	-	0.95	0.95	0.08	0.15
ER 406	0.97	0.96	0.03	0.18	-	-	-	-
ER 729	-	-	-	-	0.89	1.16	0.13	0.30

r = correlation coefficient; se(b) = standard error of slope;

b = slope of regression line; sd(res) = standard deviation of residuals.

* Significantly different from 1.0 at $p < 0.05$.

Note: All data were transformed to logarithms, and the regression lines were fitted by the least squares method.

in the 22 measurements of the mandibular data set it is perhaps not surprising that the regression line for ER 729 has a slope greater than unity. This occurs because the small measurements (near the origin on the bivariate regression) are smaller than expected, while the large measurements (furthest from the origin) are larger than expected. In contrast, the individual male Gorilla specimen yielded a regression slope significantly less than unity. This specimen is from a species in which the males have a particularly large anterior dentition, the measurements of which have probably contributed to reducing the slope of the regression line.

To summarise, after logarithmic transformation the data for different hominoid and hominid crania and mandibles could be modelled by isometric Q-mode regression against the log-transformed measurements of a hypothetical 'average primate'. In this regression model, the average size difference between a test specimen and the 'average primate' is given by the regression intercept on the dependent axis. The difference in shape between the test specimen and the 'average primate' is given by the set of positive and negative residuals from the reression line. Each residual contains the shape information carried by a single measurement.

Kazmierczak's transformation

By assuming average isometry between test and reference specimen measurements one can justify constraining the slope of the Q-mode regression line to equal unity. The residuals from this regression are given by the formula:

$$r_i = y_i - x_i - (y_{mean} - x_{mean})$$

where y_i and x_i represent the ith log-transformed measurements of the test specimen (y) and reference specimen (x), and

y_{mean} and x_{mean} are the means of the log-transformed test specimen and reference specimen measurements respectively, and

r_i is the residual for the ith log-transformed test taxon measurement (see Figure 3.04).

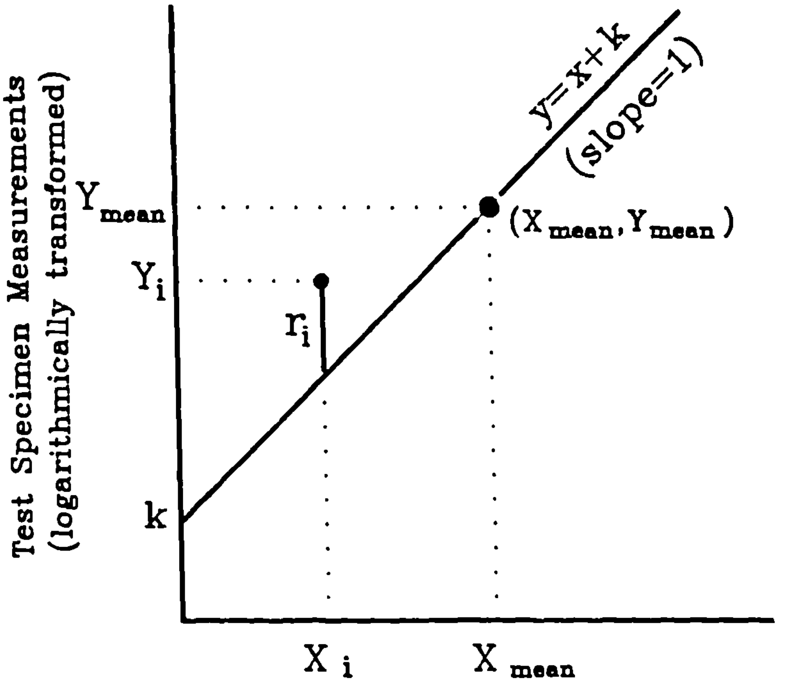
The above formula is mathematically equivalent to a transformation proposed by Kazmierczak (Kazmierczak, 1985; Berge and Kazmierczak, 1986), and is hereafter referred to as 'Kazmierczak's transformation' (the only difference between the approach adopted here and that taken by Kazmierczak lies in the latter author's use of the complete data matrix to calculate the values for the reference specimen).

When translated back into the units of raw measurement, each value given by Kazmierczak's transformation is equivalent to the expression

$$R_i = (Y_i/X_i) / (Y_{g.mean}/X_{g.mean}).$$

In terms of the raw measurements, this is the ratio of the test specimen measurement to the reference specimen measurement divided by the ratio of the geometric means of all the test specimen and reference specimen measurements. Note that the geometric mean

Figure 3.04 Residuals from logarithmic isometric regression



Reference Specimen Measurements
(logarithmically transformed)

<u>Derivation of Kazmierczak's Transformation</u>

$$r_i = y_i - (x_i + k)$$

$$r_i = y_i - x_i - (y_{mean} - x_{mean})$$

reduces to the arithmetic mean on logarithmic transformation, and that these ratios are in Q-mode (between taxa), not R-mode (between variables). It can easily be seen that the above expression satisfies the criterion of Mosimann (1970) and Hills (1978) for a true shape function. When all Y are changed in the same proportion then Y_i (a given test specimen measurement) and $Y_{g.mean}$ (the geometric mean of test specimen measurements) will change in the same proportion and the ratio R_i will remain unchanged. The set of ratios $R_1 \ldots . R_n$ comprise a true shape function since they are invariant to isometric change in the test specimen. It is further assumed here that the set of log-transformed ratios given by Kazmierczak's transformation ($r_1 \ldots . r_n$) likewise constitute a valid shape function, in the sense defined by Mosimann (1970) and Hills (1978).

A further advantage of Kazmierczak's transformation is that it is little affected by missing data. Least-squares regression is sensitive to some data points off the major axis of the bivariate distribution (such points are referred to by Atkinson (1985) as 'points of high leverage'). Unlike least-squares regression, the values given by Kazmierczak's transformation are influenced only by changes in the differences between the <u>means</u> of the dependent and independent variates (that is, by changes in $y_{mean} - x_{mean}$, the grand means of the log-transformed test and reference specimen measurements). The calculations involved in computing the transformation are simple, and, even for large data sets, can be carried out on a microcomputer using commercially available spreadsheet programs. The method also provides a measure of the overall size of the test specimens relative to the reference specimen.

3.3.3 Taxonomic discrimination using Kazmierczak's transformation

Species and sex differences in transformed values

Estimates of morphological similarity based on raw measurements may be poor indicators of taxonomic affinity because of the confounding effects of size variation within and between species. For this reason the effects of size may have to be reduced or eliminated prior to making quantitative taxonomic comparisons. The efficacy of the Kazmierczak's transformation in removing size and recovering taxonomic information was investigated by comparing phenetic classifications of separate sex samples of extant primate taxa, before and after applying the size reduction method to the raw measurement data.

The sample of primate taxa used in this study included some of the most dimorphic species among living primates (see Clutton Brock *et al.*, 1977 for values of sexual dimorphism in extant primates). In sexually dimorphic primates the male and the female skulls differ both in size and in shape. Shape differences are prominent in the ectocranial superstructures (which were not measured in this study) but are also evident in other aspects of the cranial skeleton, for example in the relative sizes of the teeth (Wood, 1976b, 1979). Dental measurements form a substantial part of the data collected in this study, and it was therefore of interest to see whether the use of Kazmierczak's transformation would remove enough of the size-related morphological difference between the sexes in the dimorphic primates to allow their correct phenetic classification.

Average linkage (UPGMA) cluster analysis was carried out on the sex-specific mean measurements of six non-human primate taxa and modern *H. sapiens*. The complete data set of 90 linear measurements (cranial, mandibular and dental variables) was used, and the analysis was carried out separately on raw measurements and transformed values calculated as shown above. The cluster analyses were carried out on the IBM installation at the University of Liverpool, using the GENSTAT package to create dendrograms from a matrix of similarities. Similarities were calculated as (1 - Pythagorean Distance).

The UPGMA cluster of the 14 sex/species units was unsatisfactory (Figure 3.05). The clustering based on the raw data grouped female *Pongo* with male and female *Pan*, but male *Pongo* was placed closer to *Gorilla*. *Colobus* and *Hylobates* were grouped as one cluster at the same level of similarity (the latter taxa are small-skulled species with little sexual dimorphism). In the dimorphic taxa *Papio*, *Gorilla* and *Pongo* the sexes were relatively dissimilar, and in these taxa the sexes were in fact less similar than some separate pairs of species (e.g. *Colobus* and *Hylobates*, or *Pan* and female *Pongo*).

The sex-specific mean measurements sets for the seven taxa were subjected to Kazmierczak's transformation using the Symphony spreadsheet program running on an IBM-PC compatible microcomputer. The transformed values were then read into GENSTAT for cluster

Figure 3.05 UPGMA cluster based on sex–specific mean raw cranial dimensions in seven extant primate taxa. Ninety variables were included in the analysis.

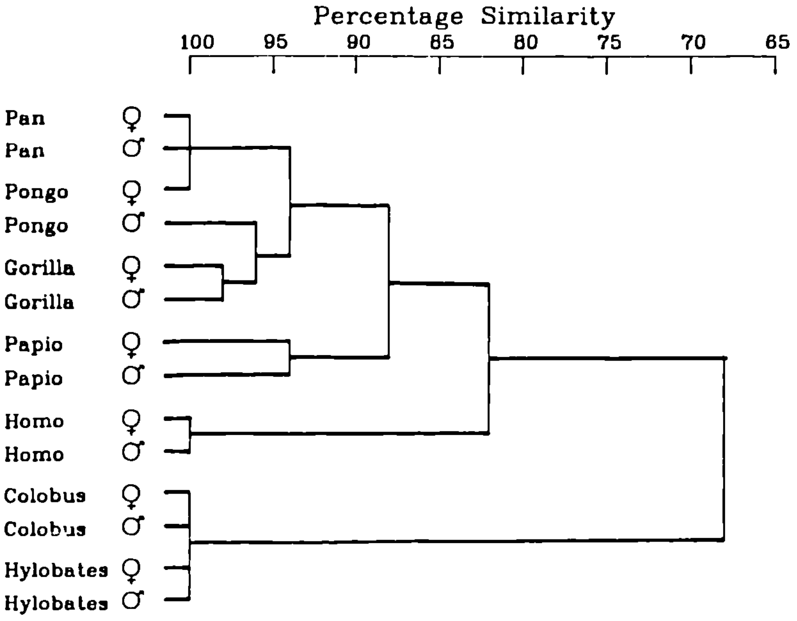
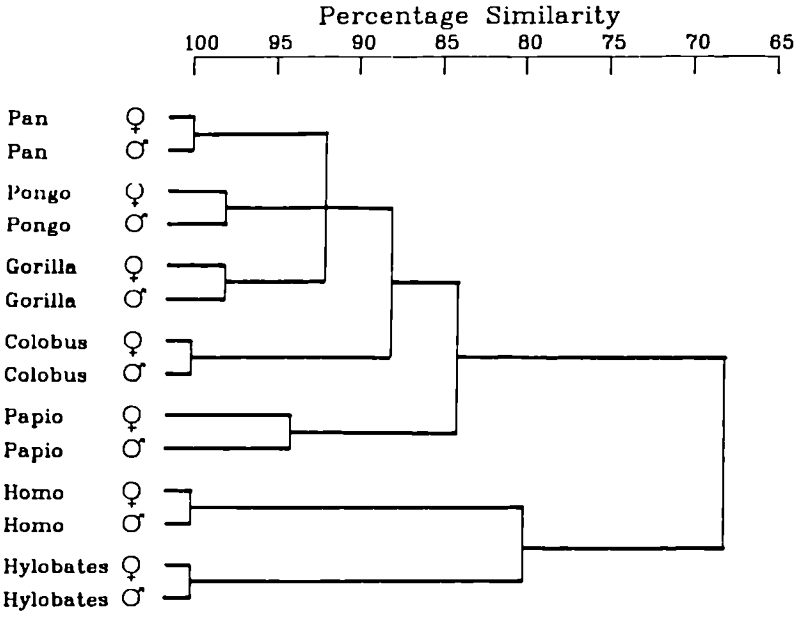


Figure 3.06 UPGMA cluster based on sex–specific mean dimensions after Kazmirczak's transformation. Ninety variables were included in the analysis.



analysis. The UPGMA grouping based on the transformed values (Figure 3.06) revealed a more satisfactory pattern of similarities between and within taxa. The dimorphic taxa were still characterised by relatively low between-sex similarity, but in every instance the sexes of these dimorphic taxa were correctly classified. Furthermore, in *Papio*, which possessed the least similar sexes, the males and females were nonetheless more similar to each other than were the most similar distinct species (*Pan*, *Pongo* and *Gorilla*). The relatively low between-sex similarity in the dimorphic species may result from there being a residue of allometrically-determined shape difference which Kazmierczak's transformation is not able to remove from the data. In common with other phenetic classifications of primate skulls, the cluster analysis of these taxa (even after reduction of size differences) produced a great ape cluster, with *H. sapiens* grouped with *Hylobates* (c.f. similar results in Creel, 1986).

The UPGMA clustering of raw and transformed data was also compared in a smaller measurement set by restricting the analysis to 22 measurements taken on the mandible. The dendrogram for raw mandibular measurements (Figure 3.07) misclassified the sexes of the *Papio* and *Pongo*, while the transformed values (Figure 3.08) allowed a correct phenetic classification of all sex/species combinations. However, in the cluster transformed mandibular data the between-sex similarity in one species (*Papio*) was quite low, and the dendrogram no longer featured a separate great ape cluster.

Taken together, these results support the view that the technique of

Figure 3.07 UPGMA cluster based on sex-specific mean raw mandibular dimensions (22 variables)

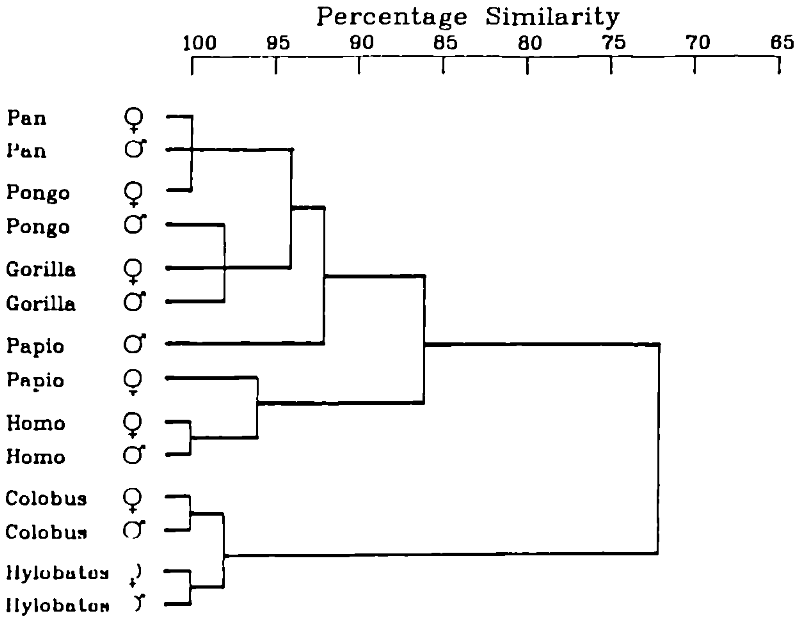
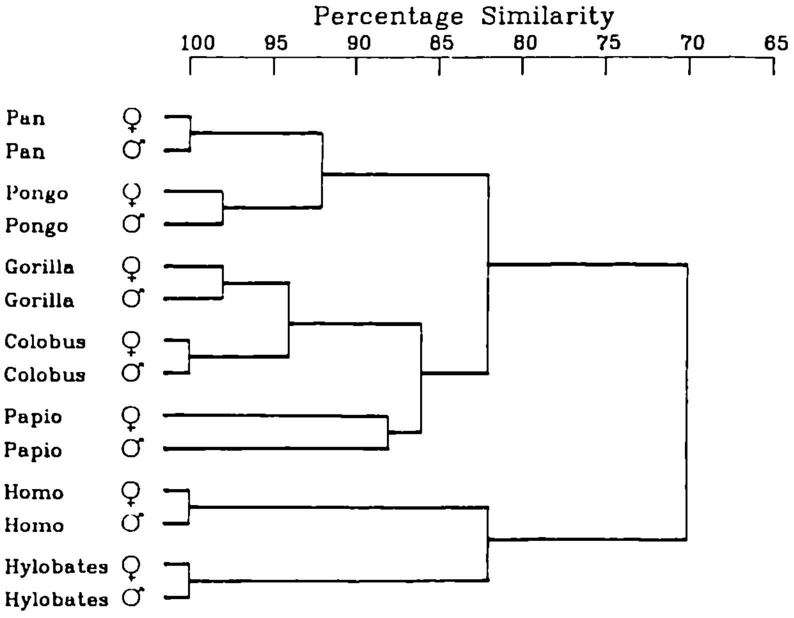


Figure 3.08 UPGMA cluster based on sex-specific mean dimensions after Kazmierczak's transformation of mandibular data (22 variables included in analysis)



taxonomic comparison using Kazmierczak's transformation, when applied to mean measurements taken on extant primate taxa, can overcome potential problems of size variation and intraspecific allometry. When applied to the complete measurement sets of cranial, mandibular and dental measurements, the technique yielded a measure of morphological similarity which consistently placed female primates closest to their conspecific males. It remained to be shown, however, that individuals, of either sex, could be correctly allocated to species using this method.

Intraspecific and interspecific individual variation

Raw measurements for individual primate specimens were also subjected to Kazmierczak's transformation in order to investigate the pattern of intraspecific and interspecific variation among individuals. Such an investigation was regarded as an essential precursor to an analysis of fossil hominids. Conclusions based on comparisons between mean values (such as the tests described above) may not be relevant to the palaeontological situation where the taxonomic affinities of specimens may be unknown, and where taxa may have to be delineated on the basis of comparisons between individual specimens.

Prior to making the comparisons between the individuals the transformed data were converted from continuous variables into discrete character states. Although this results in a loss of information, the loss was minimised by allowing the transformed data each variable to occupy up to nine character states. The conversion to character states was carried out by dividing each transformed value by a fixed value (0.04; the value was determined empirically), discarding fractions of a unit and then adding four units. This transformation (of a type referred to as 'combination coding' by Sokal and Rohlf, 1981) ensured that the transformed data were converted into character states that were positive integers between the inclusive limits 0 and 8, with a mean value of 4. Thus a value of zero was coded as 4, and positive values were coded as 5, 6, 7 or 8 according to their magnitude; negative values were likewise coded as 3, 2, 1 and 0, depending on their magnitudes. No attempt was made to standardise for the different ranges of the transformed values found in different variables. It was assumed that any variables yielding a narrow range of transformed values were evolutionarily conservative among these taxa, and under the procedure adopted here such variables would occupy few of the available character states. Conversely, variables which gave a wide range of transformed values in different individuals or taxa would occupy a correspondingly wide range of the available character states. Very large positive or negative transformed values, that would otherwise have exceeded the chosen range of character states, were coded as the maximum (8) or minimum (0) character states respectively.

Coding the transformed values as character states allowed a simple measure of morphological distance to be used - Mean Character Difference (Cain and Harrison, 1958). This measure, which is related to the Manhattan distance, is the average of the absolute values of character differences calculated for all available characters. The calculation was made using an option provided in the PAUP phylogenetic program which allows the determination of character difference matrices between taxa or between specimens (Swofford, 1985). PAUP was used because it has the facility for pairwise deletion of missing values, an essential requirement here since the same procedure was to be used to compare incomplete fossil specimens with each other.

Five male and five female specimens were selected at random from each of the seven extant primate taxa for which data had been obtained. This subsample of the total comparative data set (amounting to half of the available specimens) was chosen because it was large enough to allow a sufficient number of within-sex, between-sex and between-species comparisons to be made among individuals. Within each primate species comparisons were made between each pair of specimens in the subsample, thus a total of 10 between-male, 10 between-female and 25 between-sex comparisons were made within each primate species. Between-species comparisons were made among a further reduced sample comprising one specimen of each sex randomly selected from within each species. Each of these latter specimens was compared to the male and female specimen of all other taxa, thus a total of 24 between-species comparisons was made for each species. Separate calculations were carried out for the cranium and the mandible, and the results (mean values and range of variation for within-male, within-female, between-sex and between-species comparisons) are given in Figures 3.09 and 3.10.

Figure 3.09 shows that, for the crania of these taxa, there is usually a clear distinction between the maximum intraspecific Mean Character Difference (MCD) and the minimum interspecific MCD. The

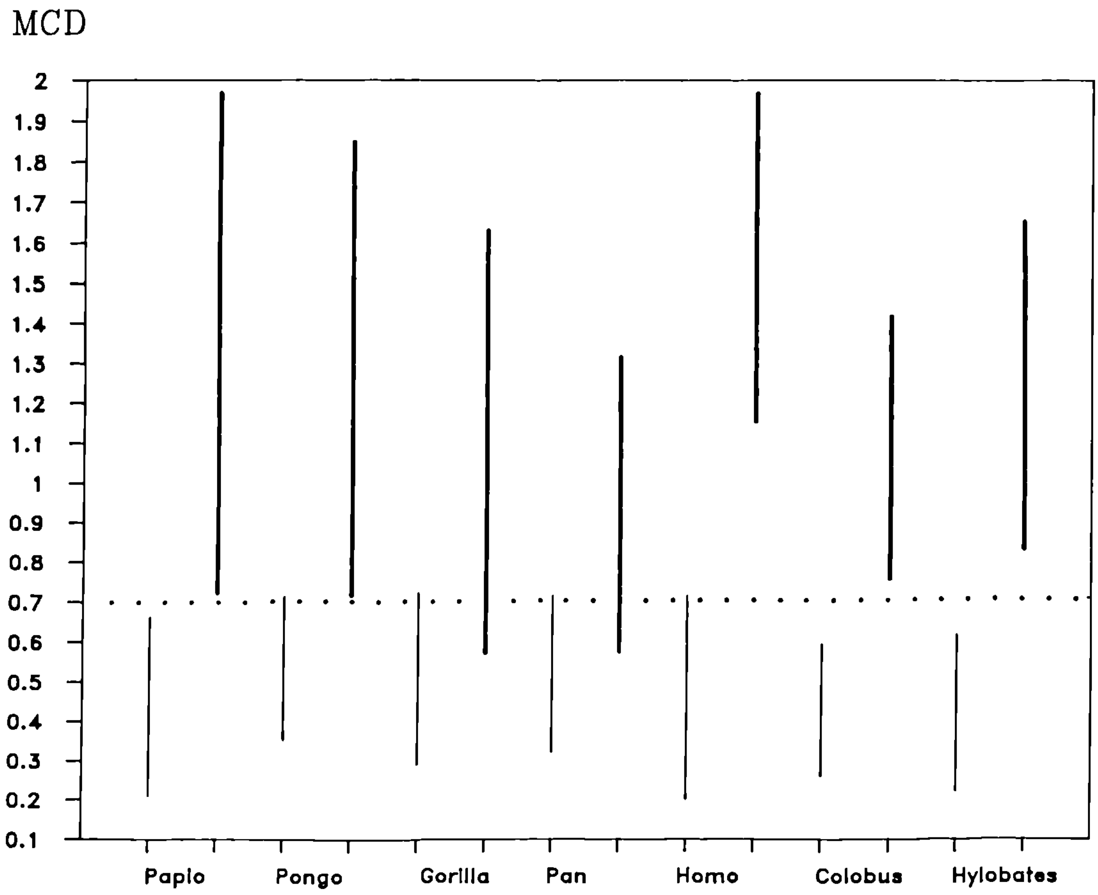


Figure 3.09 Range of Mean Character Difference (MCD) within and between extant primate species, based on 68 cranial characters. Data include within and between sex comparisons; the narrow bars indicate the range of MCD within a species while the broad bars indicate the range of MCD for all comparisons between that species and six other species. The dotted line indicates the approximate upper limit of within-species variation.

maximum value of MCD of 0.7 is only exceeded when the specimens being compared belong to different species: differences of this magnitude are not found even within the dimorphic species. Conversely, an MCD of less than 0.7 nearly always indicates that the specimens being compared belong to the same species. One interspecific comparison (out of 84 such comparisons conducted here) yielded a Mean Character Difference of less than 0.7 (this was between one Pan and one Gorilla skull, and is responsible for the lower limit of MCD = 0.57 observed for interspecific comparisons involving these two taxa.

Within each taxon there is little tendency for between-sex distances to be greater than within-sex distances (with the exception of Papio). The minimum distances between specimens varied between taxa, and tended to be less in the monomorphic taxa Homo, Colobus and Hylobates. The most similar specimens were found in Homo and Hylobates, but the minimum intraspecific distances in most taxa were about 0.2 or 0.3. This lower limit for between-specimen distance may reflect a combination of statistical 'noise' and the effects of stochastic individual variation. The largest between-specimen distances resulted from making between-species comparisons involving Papio or Homo.

A similar, but less distinctive pattern was observed when mandibular data was used as the basis for comparison (Figure 3.10). Again, for most taxa there appeared to be a maximum limit on intraspecific variation corresponding to a Mean Character Difference of 0.9. This limit was exceeded in the highly sexually dimorphic taxa Papio and Gorilla, in which larger intraspecific differences were seen.

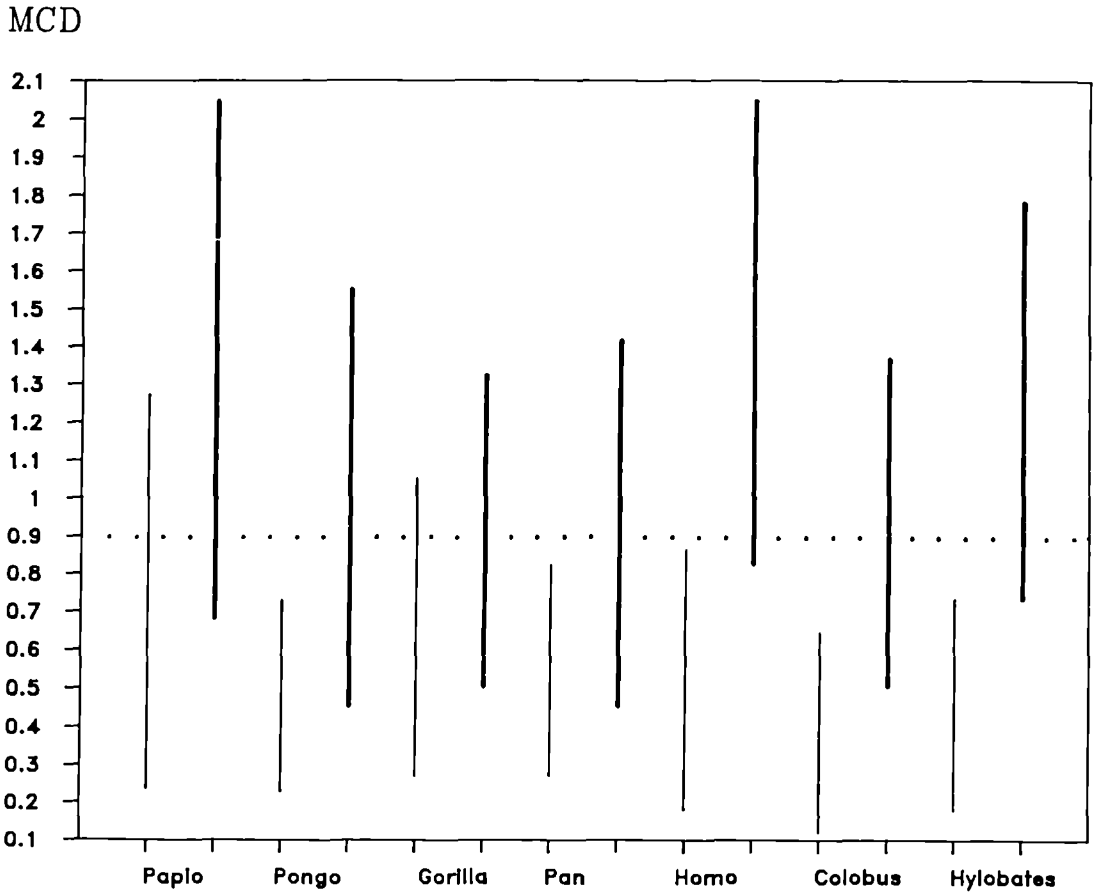


Figure 3.10 Range of Mean Character Difference (MCD) within and between extant primate species, based on 22 mandibular characters. Key as for Figure 3.09.

Furthermore, for several primate species (Pongo, Gorilla, Pan, Colobus) interspecific comparisons yielded MCD values of less than 0.7. In all dimorphic species there was overlap between intra- and interspecific distances. However, it could be concluded from these mandibular data that a between-specimen MCD of greater than 0.9 is only found within highly dimorphic taxa (e.g. Papio and Gorilla), and is more often indicative that the specimens being compared belong to different species.

Effect of missing data on comparisons between individuals

The numerical comparisons made between specimens can be affected if the specimens do not have a full set of data. This is a particularly prominent difficulty in comparing fossil specimens, which are often incomplete. Both the calculation of Kazmierczak's transformation, and the comparison between specimens using Mean Character Difference, may be influenced if specimens lack the relevant measurements. Kazmierczak's transformation, on which comparisons made in the present study depend, is only influenced by missing data if the latter result in disproportionate changes in the means of the specimen and reference measurements (see above). Comparisons between specimens will be further influenced because missing measurements will also result in the loss of the corresponding character state data. Two specimens can only be compared on characters for which data are present for both specimens. Since some characters tend to be conservative, while others are divergent, the availability of characters may influence the measure of distance (Mean Character Distance) employed in this study.

The effect of missing data was investigated by making test comparisons between complete crania, and then recalculating the data transformations and character states for these specimens after deleting different (but representative) portions of their data. The test comparisons were made between two *Colobus* crania, between a *Colobus* and a *Hylobates* cranium and between a *Colobus* and a *Homo* cranium. The species were chosen so that the effect of missing data on within-species and between-species comparisons could be determined, with the interspecific comparisons involving lesser and greater degrees of size difference.

Initially, the raw data were transformed and character states were calculated, in the usual way, for the complete data sets for these crania. Representative pairs of fossil hominids were then chosen as a basis for simulating missing data. The fossil hominid pairs were selected so that the number of measurements present in both members of a pair of fossils varied from about 25% to about 75% of all measurements. Taking each pair of fossils in turn, the residuals and character states for the *Colobus* - *Colobus*, *Colobus* - *Hylobates* and *Colobus* - *Homo* comparisons were then recalculated using only the data that corresponded to the measurements present in the fossil hominid pairs. Thus, using the first pair of hominids (ER 1813 and OH 13), the data set for one *Colobus* cranium was reduced until it only contained measurements also present in ER 1813, while the other *Colobus*, the *Hylobates* and the *Homo* data sets each were reduced to measurements present in OH 13. The data transformation and character states were then recalculated for the reduced data sets. The whole procedure was repeated using four other representative pairs of fossil hominids (ER 1813 and ER 1470, ER 406 and ER 732, Sts 5 and Sts 71, Petralona and Kabwe). The Mean Character Differences given by these simulations of missing data are listed in Table 3.07.

The effects of comparing specimens on a restricted range of characters that were themselves recalculated from reduced sets of raw measurement data are variable, and depend both on the characters involved and the specimens compared. The changes in Mean Character Difference resulting from missing data are more marked in the comparisons between Colobus and Homo than they are in the comparisons within Colobus, but the smallest effect occurs in the comparisons between Colobus and Hylobates. Inspection of the complete set of character states for Colobus and Homo showed that these specimens differed greatly in their vault characters (MCD = 2.92) but much less in the characters of the face (MCD = 0.58). Thus it is possible that missing data may differentially eliminate characters from these two regions, and thereby have a marked effect on the overall similarity between these specimens. The change in MCD under conditions where data were missing was much greater for the Homo-Colobus comparison than it was for the Colobus-Colobus or the Colobus-Hylobates comparisons. There was still appreciable variation in the Mean Character Difference for comparisons between the two Colobus crania, but these specimens would nonetheless have been considered to be conspecific using the criteria established above.

Conclusions on taxonomic applications of Kazmierczak's transformation

TABLE 3.07

Mean character differences for comparisons between single primate crania using patterns of missing data typical of hominid fossils

Model for Missing data	All Data	ER 1813/ OH 13	ER 1813/ ER 1470	ER 406/ ER 732	Sts 5/ Sts 71	Kabwe/ Petralona
(Data present)	(68)	(15)	(32)	(18)	(39)	(50)
Colobus-Homo	1.31	1.93	1.28	1.17	1.56	1.14
Colobus-Hylobates	1.09	1.13	1.06	1.00	1.02	1.04
Colobus-Colobus	0.46	0.67	0.59	0.50	0.67	0.66

Note: The different columns show the effects on MCD estimates for pairs of primate crania using different, representative patterns of missing data. The models for the patterns of missing data were pairs of hominid fossil crania.

Overall, some conclusions can be drawn from this analysis of the pattern of variation in character states based on data subjected to Kazmierczak's transformation. When a large number of characters are sampled the Mean Character Difference between specimens appears to be limited within any one species. In this data set, comprising measurements on a range of extant primates, there is a reasonably clear distinction between intraspecific and interspecific distances when the larger set of cranial measurements is utilised. The maximum value of Mean Character Difference for intraspecific comparisons of cranial characters is 0.7. A slightly higher limit (0.9) is seen in some taxa when comparisons are based on the smaller set of mandibular measurements, but in the dimorphic taxa _Papio_ and _Gorilla_ this limit is exceeded for the mandibular comparisons. Between-species comparisons based on cranial data usually yield Mean Character Differences greater than 0.7, but between-species comparisons based on mandibular data sometimes fall as low as 0.45. Clearly, the measures of interspecific difference would have been lower if one had chosen primate taxa which were morphologically less distinct than the ones analysed here (for example, some comparisons between congeneric species would probably fall within the range of intraspecific variation).

Since the empirically determined limits for intraspecific variation are based on comparisons in a range of anthropoid taxa, and seem to be reasonably robust to missing data, there seems to be no _a priori_ reason why they should not be used as a basis for investigating species limits in fossil hominids. It should, however, be remembered that data collected from fossils are often of a lower quality than that obtained from non-fossil material, and that missing data will introduce some uncertainty into quantitative comparisons using this method (Table 3.07).

3.3.4 The use of k as a measure of size

As noted above, in a Q-mode regression with unit slope, carried out on log-transformed test and reference data, the y-intercept (k) gives a measure of the relative overall size of the test specimen. The value of k is equal to the difference between the means of the log-transformed test specimen measurements and the log- transformed reference measurements: $k = y_{mean} - x_{mean}$. In the scale of raw measurement, antilog (k) is equivalent to the ratio of the geometric means of the test specimen measurements and the reference measurements: antilog $(k) = (Y_{g.mean} - X_{g.mean})$. Thus the size of two specimens can be compared directly by calculating the difference between their respective values of k:

$$k_2 - k_1 = (y_{2mean} - x_{mean}) - (y_{1mean} - x_{mean}) = y_{2mean} - y_{1mean}.$$

The latter expression, in units of raw measurement, is equivalent to $Y_{2\ g.mean} / Y_{1\ g.mean}$, or the ratio of the specimen means. The range of values of k for a given taxon is equivalent (in units of raw measurement) to the ratio of the overall sizes of the largest and smallest specimens in that taxon.

In morphometric studies of primates the ratio of the female mean to

TABLE 3.08

Average values of k (logarithmic relative size) and values of dimorphism for samples of extant primates

	k_{male}	k_{female}	$(k_{female}-k_{male})$	Dimorphism	
				This study*	Wood (1976b)
Papio	0.026	-0.060	-0.086	0.82	0.84
Colobus	-0.170	-0.209	-0.038	0.92	0.91
Hylobates	-0.235	-0.242	-0.008	0.98	-
Pongo	0.105	0.042	-0.063	0.87	-
Pan	0.043	0.029	-0.014	0.97	0.94
Gorilla	0.143	0.106	-0.037	0.92	0.87
Homo	0.048	0.030	-0.018	0.96	0.95

*Dimorphism = female size / male size = antilog $(k_{female} - k_{male})$

Values from Wood (1976b) are the averages of his separate mean values 'all teeth', 'mandible', 'face/palate' and 'skull', based on 34, 17, 15 and 13 measurements respectively.

the male mean has been used as an index of sexual dimorphism (cf. Wood, 1976b). An average value for sexual dimorphism in the primates studied here can be obtained by evaluating the expression: antilog $(k_{\text{mean female}} - k_{\text{mean male}})$. This expression has been calculated for the seven extant primates included in this study, and the results (Table 3.08) have been compared with the values of average cranial dimorphism reported for five of these taxa by Wood (1976b). The values reported here are similar to those determined by Wood (1976b), who used 79 cranial and dental measurements. The largest departure from Wood's results is seen in *Gorilla*, where my estimate of dimorphism (0.92) indicates less marked dimorphism in this taxon than is reported by Wood (0.87). The difference between our results for this taxon is attributable to the fact that smaller than average male specimens were selected in my study, in order to ensure that vault measurements could be recorded accurately on the male crania. Overall, these findings indicate that k is indeed an appropriate measure of relative size in these specimens.

The values of k were also calculated for individual primate specimens in order to estimate the range of intraspecific variation in relative size. The same samples of males and females that were used in the estimates of similarities (see above) were used for this purpose. The ranges of k for the male and female subsamples are depicted, for crania and mandibles separately, in Table 3.09 and Figures 3.11 and 3.12. Note that k is a logarithmic expression of relative size, and thus linear difference in k is equivalent to proportional difference in specimen size. The largest range of k was seen in the most dimorphic taxa, *Papio* and *Pongo*. These ranges, based on balanced-sex

TABLE 3.09

Mean and range of variation in k (logarithmic relative size) in balanced sex samples of crania and mandibles of extant primates

		Cranial Size (68 variables)			Mandibular Size (22 vbles.)		
Taxon		Male	Female	Both sexes	Male	Female	Both sexes
PAN	(Mean)	.034	.026	.030	.028	.023	.026
	(Max.)	.055	.040	.055	.057	.031	.057
	(Min.)	.022	.008	.008	.007	.006	.006
	(Range)	.033	.032	.047	.050	.025	.051
PONGO	(Mean)	.064	.033	.049	.121	.077	.099
	(Max.)	.096	.052	.096	.143	.098	.143
	(Min.)	.048	.016	.016	.093	.066	.066
	(Range)	.048	.036	.080	.050	.032	.077
GORILLA	(Mean)	.116	.096	.106	.142	.112	.127
	(Max.)	.135	.112	.135	.168	.120	.168
	(Min.)	.096	.079	.079	.117	.101	.101
	(Range)	.039	.033	.056	.051	.019	.067
HOMO	(Mean)	.070	.056	.063	-.007	-.024	-.016
	(Max.)	.080	.073	.080	.009	-.017	.009
	(Min.)	.053	.036	.036	-.020	-.028	-.028
	(Range)	.027	.037	.044	.029	.011	.037

TABLE 3.09 [Contd.]

Taxon		Cranial Size (68 variables) Male	Female	Both sexes	Mandibular Size (22 vbles.) Male	Female	Both sexes
	(Mean)	-.213	-.235	-.224	-.271	-.301	-.286
HYLOBATES	(Max.)	-.203	-.231	-.203	-.261	-.276	-.261
	(Min.)	-.227	-.241	-.241	-.291	-.320	-.320
	(Range)	.024	.010	.038	.030	.044	.059
	(Mean)	.013	-.064	-.026	.070	-.045	.013
PAPIO	(Max.)	.024	-.058	.024	.086	-.033	.086
	(Min.)	-.018	-.076	-.076	.044	-.057	-.057
	(Range)	.042	.018	.100	.042	.024	.143
	(Mean)	-.193	-.209	-.201	-.155	-.184	-.169
COLOBUS	(Max.)	-.176	-.191	-.176	-.132	-.175	-.132
	(Min.)	-.218	-.223	-.223	-.188	-.192	-.192
	(Range)	.042	.032	.047	.056	.017	.060

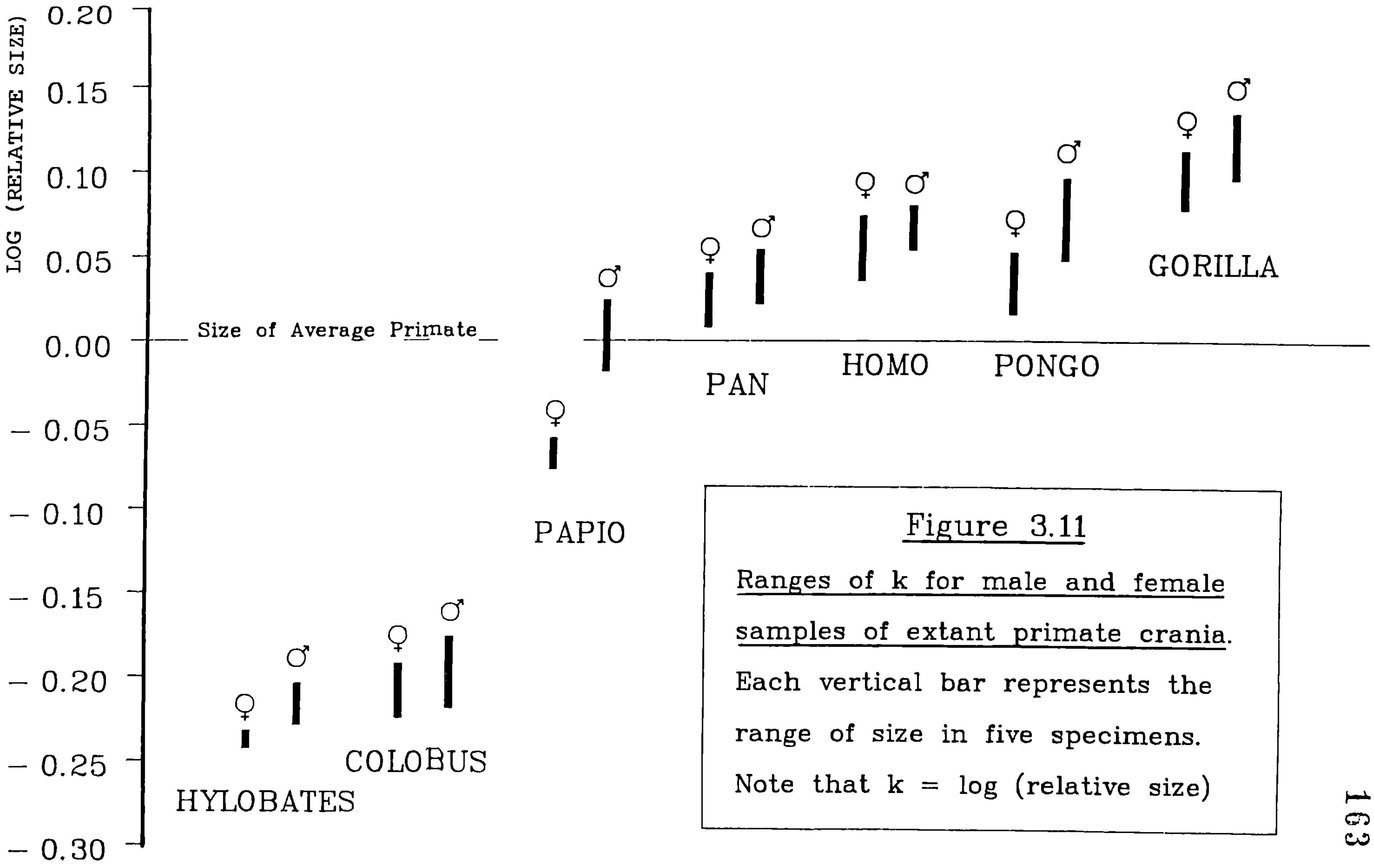


Figure 3.11

Ranges of k for male and female samples of extant primate crania. Each vertical bar represents the range of size in five specimens. Note that k = log (relative size)

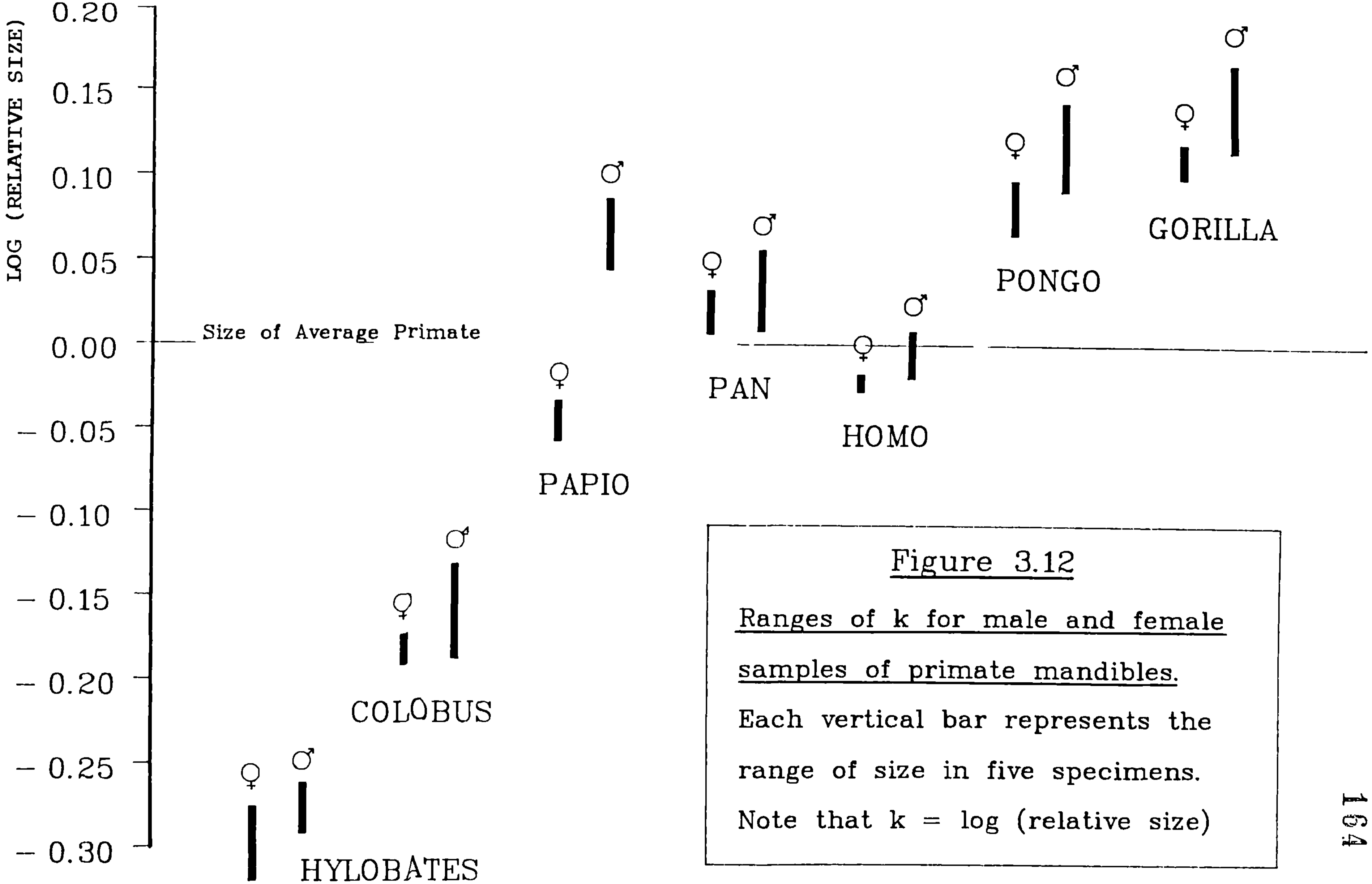


Figure 3.12

Ranges of k for male and female samples of primate mandibles.

Each vertical bar represents the range of size in five specimens.

Note that k = log (relative size)

samples of ten specimens, can be used as a guide to the expected size variation in hominid species-level taxa.

3.3.5 Methods of cladistic analysis

The numerical method of phylogeny reconstruction used in the present study is known as the 'Wagner method' (Kluge and Farris, 1969; Fitch, 1971). The aim of the Wagner method is to use character state data to find the minimum length bifurcating network, or tree, that connects a group of taxa. The measure of length is the Manhattan metric, which expresses the distance between two adjacent nodes of the network as the sum, across all characters, of the absolute differences in their character states. In the Wagner tree the OTUs in the analysis appear as terminal taxa, while the internal nodes of the tree are reconstructions of hypothetical 'ancestral' OTUs. The length of the tree is defined as the sum of the lengths of all the individual branches of the tree, and the most parsimonious tree is the tree of minimum length.

A Wagner tree will usually differ from a phenetic dendrogram for the same group of taxa. Phenetic dendrograms are based on similarities between OTUs, while Wagner trees are based on parsimonious interpretations of character evolution among OTUs. The different methods will give the same results only if the rate of character evolution is the same (and divergent) along all branches of the phylogeny (Farris, 1970). Of the available Wagner methods, maximum parsimony analysis is to be prefered to compatibility methods because, in my view, the latter are prone to give trees that are based on convergence rather than on homology.

The cladograms in this study were computed using the PAUP phylogeny program (Swofford, 1985). This program initially produces unrooted minimum length trees (Wagner trees). The trees can then be rooted to form cladograms, and several methods of rooting are allowed by the program. One or more of the OTUs in the analysis may be designated as an 'outgroup', in which case these taxa are placed as the sister group of the remaining taxa (the 'ingroup') in order to root the tree (subject to the constraint that the ingroup must be monophyletic). Alternatively, the ancestral character states for the whole group can be determined independently, and the minimum length tree can then be rooted at a point closest to the inferred ancestral morphotype. This method is referred to as 'Lundberg rooting' (Maddison et al., 1984; Swofford, 1985). As a variant of the first method, a hypothetical ancestor or outgroup can be reconstructed in a separate analysis, then included with the ingroup taxa before determining the minimum length tree for the ingroup and ancestor together. This tree can then be rooted by making the hypothetical outgroup the sister group of all other taxa (Maddison et al., 1984).

The latter procedure (inclusion of a hypothetical outgroup) was followed in the present study. There were two main advantages in adopting this approach. Firstly, the task of finding the most parsimonious tree would have become much more difficult if, in addition to the ingroup taxa, several outgroup taxa were also to be included in the analysis. The number of possible trees for a group of taxa increases very rapidly as a function of the number of taxa (Table 3.10), and if more than 10-12 taxa are included in the analysis PAUP cannot guarantee that the shortest tree will be found. Secondly, by analysing the outgroup taxa separately, the additional homoplasy present among the outgroup taxa will have little influence on the most parsimonious solution for the ingroup taxa. The hypothetical outgroup was included in the parsimony analysis, rather than simply providing character states for Lundberg rooting, because the latter method appears to lack precision if all ingroup taxa are unlike the hypothetical ancestor.

The hypothetical hominid ancestor was reconstructed from an independent character analysis among the non-human primate species included in the study. Advantage was taken of the consensus that now exists on the phylogeny of these taxa, a consensus that is supported by the results of over 25 years of molecular studies (Goodman, 1961; Miyamato & Goodman, 1986). Maddison et al. (1984) have shown that when the phylogeny of a set of outgroup taxa is known, this information can be used to make a more accurate estimation of the ancestral morphotype for the ingroup than can be achieved by assuming that character states common among the outgroup are necessarily primitive. Algorithms provided by Farris (1970) and Fitch (1971) establish the most parsimonious pattern of character state evolution for a known phylogeny.

Using the PAUP program, the character states for the outgroup taxa were 'optimised' on the known (i.e. molecular) outgroup tree (the term 'optimisation' refers to any parsimonious interpretation of

TABLE 3.10

Increase in the number of possible unrooted trees with increasing number of OTUs

No. of OTUs	No. of Trees
3	1
4	3
5	15
6	105
7	945
8	10,395
9	135,135
10	2 million
11	34 million
12	650 million
13	1.4×10^{10}
14	3.2×10^{11}
15	7.9×10^{12}

Number of trees for n taxa is given by the series:

$1 \times 3 \times 5 \times \ldots (2n - 5)$

(formula taken from Penny, 1982).

ancestral morphotypes). The character states for the node immediately ancestral to Pongo, Pan and Gorilla were then selected on the grounds that this node was a reasonable approximation to the ancestral hominid morphotype. The node ancestral to the African great apes could have been chosen instead of the node ancestral to all great apes. However, this would have implied that hominids were more closely related to either one or the other of the African apes. Although some molecular cladograms support the view that hominids are most closely related to Pan among living non-human animals (Hasegawa et al., 1984; Sibley and Ahlquist, 1984; Bishop and Friday, 1985) the issue is still debateable, both from the morphological perspective (Groves, 1986) and from a consideration of a spectrum of molecular evidence (Andrews, 1986; Savatier et al., 1987). While the possibility remains that there is an African ape clade it is to err on the side of caution to select the adjacent but more distant node on the molecular cladogram as that characterising the ancestral hominid morphotype. Thus the character states constituting the morphotype of all three great apes was chosen as the hypothetical ancestor that was included in the parsimony analyses of the ingroup taxa.

The character states used in constructing the cladograms were the same as those used to make comparisons between individual specimens (see above). For the purposes of increased accuracy, when several hominid specimens were grouped together in one taxonomic unit their transformed characters were averaged prior to calculating the character states for that taxon. PAUP is also able to determine the character states of all nodes on the ingroup tree. The character states defining these internal nodes include the synapomorphies that define the ingroup clades or higher taxa. Several methods of searching for a most parsimonious tree are available in the PAUP phylogenetic program, but in every instance I used the branch-and-bound method, which ensures that the shortest tree is always found.

For some of the hominid taxa no data are available for certain characters, and these were entered as missing values in the character state matrix. PAUP treats missing values as 'any possible value'. Thus the location of a taxon on a PAUP maximum parsimony tree is determined only by the non-missing data values.

CHAPTER 4: COMPARISONS OF FOSSIL HOMINIDS

4.1 Comparison by overall shape

4.2. Comparison by overall size

4.3 Detailed comparisons between H. habilis and Homo sp.

CHAPTER 4. COMPARISONS OF FOSSIL HOMINIDS

4.1 Comparison by overall shape

4.1.1 Within-group shape variation

The raw measurements of 27 fossil hominid crania and 40 hominid mandibles were corrected for size difference using Kazmierczak's transformation, and then converted into character states using the procedure detailed in the previous chapter. Matrices of mean character difference for all possible pairwise comparisons of the specimens were obtained using the PAUP phylogenetic program (Tables 4.01 and 4.02). These matrices were examined to determine whether the range of shape variation within the conventional species-level groupings of these hominid fossils resembled the range of variation observed in the extant primate samples.

The average, the maximum and the minimum within-group values of Mean Character Difference (MCD) among the crania and mandibles of the conventional taxonomic groups of fossil hominids are listed in Table 4.03. Several of the fossil groups exhibited a maximum MCD that exceeded the maximum level observed in extant primate species. The empirically-determined maximum MCD for cranial comparisons within extant primate species (MCD = 0.7) was exceeded in *H. habilis*/'early' *Homo*, 'archaic' *H. sapiens* and *A. boisei*. For mandibular comparisons the empirical maximum value (MCD = 0.9) was exceeded in *H. habilis*/ 'early' *Homo*, in *A. africanus* and in *A boisei*.

TABLE 4.01

Character difference matrix for individual hominid cranial comparisons

Values are Mean Character Differnce (MCD). For each pair of specimens the character state differences were averaged across all characters which were present in both specimens.

Specimen	OH 13	OH 24	ER 1470	ER 1805	ER 1813	SK847	Stw53	Sts5	Sts71
OH 13	0.00								
OH 24	0.21	0.00							
ER 1470	1.00	0.64	0.00						
ER 1805	0.73	0.64	0.27	0.00					
ER 1813	1.00	0.61	0.44	0.69	0.00				
SK 847	1.00	0.69	0.62	0.69	0.60	0.00			
Stw 53	1.20	0.88	0.42	0.61	0.61	0.50	0.00		
Sts 5	0.56	0.61	0.47	0.59	0.67	0.71	0.76	0.00	
Sts 71	1.00	0.71	0.74	0.76	0.60	0.68	0.53	0.56	0.00
AL comp	0.57	0.65	1.25	0.68	0.91	0.79	0.89	1.00	0.85
ER 732	1.00	0.80	0.67	1.29	0.67	1.00	0.62	0.40	0.50
ER 406	1.10	0.96	0.79	0.89	0.93	0.79	0.90	0.77	0.83
OH 5	1.29	1.00	0.82	0.86	0.96	0.80	0.76	0.67	1.00
SK 46	1.30	0.87	1.20	0.87	0.81	0.69	0.48	0.78	0.61
SK 48	1.00	0.59	0.65	0.50	0.63	0.75	0.58	0.58	0.61
SK 52	1.09	0.92	0.60	0.93	0.68	0.57	0.40	0.68	0.56
TM 1517	0.80	0.64	1.00	0.73	0.67	0.33	0.61	0.79	0.50
ER 3733	0.54	0.30	0.70	0.76	0.55	0.75	1.12	0.60	0.65
ER 3883	1.00	0.32	0.33	0.62	0.54	0.61	0.33	0.54	0.62
Ndutu	1.00	0.50	0.82	0.90	0.87	1.00	1.00	0.65	0.50
OH 9	1.50	0.53	0.64	0.81	0.64	0.57	0.67	0.39	0.43
Sang.4	0.67	0.54	0.77	0.70	0.58	0.94	1.16	0.73	0.90
Bodo	1.00	0.78	0.70	0.95	0.74	0.77	1.06	0.93	0.89
Kabwe	1.14	0.87	0.81	0.83	0.84	0.87	1.16	1.00	1.04
Petralona	0.93	0.77	0.79	0.81	0.88	0.84	1.09	1.07	0.98
Arago	0.92	1.06	0.54	0.79	0.76	1.00	1.20	0.93	1.18
Singa	1.20	0.63	0.75	1.00	0.85	0.91	0.71	0.88	0.89
H.sapiens	1.07	0.84	0.91	1.03	0.90	0.83	1.04	1.16	1.16

TABLE 4.01 [Contd.]

Specimen	ALcom	ER732	ER406	OH 5	SK46	SK48	SK52	TM1517
ALcom	0.00							
ER 732	0.57	0.00						
ER 406	0.81	0.67	0.00					
OH 5	0.97	0.84	0.60	0.00				
SK 46	0.89	0.57	0.71	0.50	0.00			
SK 48	0.68	0.50	0.54	0.49	0.47	0.00		
SK 52	0.75	0.25	0.60	0.56	0.47	0.62	0.00	
TM 1517	0.57	0.29	0.64	0.75	0.54	0.44	0.40	0.00
ER 3733	0.85	0.76	0.98	1.04	1.00	0.93	0.94	0.77
ER 3883	1.13	0.71	1.03	0.85	1.00	0.77	1.00	0.60
Ndutu	1.22	1.25	1.00	1.12	1.60	1.43	1.25	2.00
OH 9	0.92	0.67	1.12	0.78	1.00	0.40	1.00	1.00
Sang.4	1.00	1.20	1.31	1.28	1.29	0.79	1.36	0.93
Bodo	1.15	1.17	1.31	1.08	0.87	0.93	1.00	1.18
Kabwe	1.00	1.40	1.28	1.29	1.14	1.05	1.36	1.35
Petralona	1.00	1.26	1.33	1.51	1.05	1.05	1.30	1.29
Arago	1.19	1.07	1.14	1.36	1.35	1.27	1.36	1.43
Singa	1.53	1.00	1.48	1.17	1.40	1.08	1.00	2.00
H.sapiens	1.00	1.29	1.46	1.33	1.14	1.05	1.12	1.20

Specimen	ER 3733	ER 3883	Ndutu	OH 9	Sang.4	Bodo	Kabwe	Petralona	Arago	Singa
ER 3733	0.00									
ER 3883	0.36	0.00								
Ndutu	0.40	0.53	0.00							
OH 9	0.61	0.56	0.50	0.00						
Sang.4	0.47	0.75	0.50	0.69	0.00					
Bodo	0.74	0.83	0.73	0.69	0.95	0.00				
Kabwe	0.83	0.91	0.77	0.78	0.69	0.41	0.00			
Petralona	0.81	0.92	1.07	0.87	0.69	0.48	0.38	0.00		
Arago	0.93	0.85	0.86	0.75	0.80	0.50	0.51	0.66	0.00	
Singa	0.85	0.68	0.54	0.72	0.90	0.57	0.70	0.82	0.58	0.00
H.sapiens	0.95	1.05	0.82	0.83	1.03	0.41	0.54	0.75	0.59	0.85

TABLE 4.02

Character difference matrix for individual hominid mandibular comparisons

Specimen	OH 7	OH 13	OH 22	ER 730	ER 992	ER 1802	ER 1805	ER 3734	SK15	BK67	BK8518
OH 7	0.00										
OH 13	0.20	0.00									
OH 22	0.22	0.37	0.00								
ER 730	0.83	0.44	0.42	0.00							
ER 992	0.70	0.74	0.50	0.40	0.00						
ER 1802	0.87	0.47	0.54	0.47	0.56	0.00					
ER 1805	1.25	0.90	0.50	0.30	0.33	0.56	0.00				
ER 3734	0.50	0.67	0.67	0.62	0.75	0.56	0.50	0.00			
SK 15	0.62	0.41	0.46	0.53	0.75	0.31	0.40	0.40	0.00		
BK 67	1.33	0.87	0.91	0.53	0.50	0.57	0.40	1.00	0.79	0.00	
BK 8518	0.89	0.61	0.71	0.50	0.76	0.60	0.50	1.10	0.47	0.67	0.00
Zh.H1	0.67	0.92	0.60	0.50	0.33	0.54	0.62	0.83	0.91	0.36	0.92
Zh.K1	0.56	0.75	0.75	0.92	0.75	0.61	1.33	0.83	0.71	1.00	0.86
Sang.1	0.75	0.85	0.64	0.38	0.54	0.58	0.43	0.50	0.67	0.42	0.54
Sang.9	0.75	0.62	0.54	0.50	0.50	0.46	0.67	0.80	0.64	0.54	0.79
Arago 2	0.50	0.94	0.75	0.62	0.67	1.00	0.80	0.87	0.93	0.80	0.87
Arago13	0.43	0.56	0.71	0.36	0.56	0.60	0.37	0.90	0.73	0.69	0.57
Mauer	0.50	0.55	0.50	0.44	0.53	0.59	0.40	0.50	0.53	0.53	0.63
SK 12	1.75	1.15	0.80	0.69	0.61	0.75	0.22	0.50	0.75	0.67	0.61
SK 23	1.17	1.00	1.12	1.07	1.00	0.81	0.78	0.83	0.87	1.00	0.89
SK 34	0.73	0.71	0.73	0.69	0.71	0.36	0.75	0.58	0.47	0.67	0.81
TM 1517	0.56	0.47	0.69	0.64	0.60	0.33	0.57	0.50	0.38	0.82	0.77
ER 1482	1.17	0.87	0.67	0.69	0.67	0.53	1.00	0.75	0.67	0.80	0.81
ER 729	1.00	0.90	0.94	1.00	1.00	0.76	0.60	0.67	0.65	1.07	1.00
ER 818	1.50	1.00	0.91	0.54	0.54	0.67	0.37	0.43	0.75	0.67	0.77
ER 3230	1.17	0.79	1.07	0.87	1.06	0.50	0.70	0.91	0.56	1.00	0.94
Peninj	1.08	0.75	0.81	0.75	0.84	0.53	0.70	0.67	0.53	1.13	0.89
Sts 7	0.71	0.67	0.50	0.42	0.40	0.41	0.22	0.67	0.61	0.64	0.79
Sts 36	0.87	0.62	0.61	0.50	0.62	0.23	0.44	0.80	0.43	0.54	0.57
Sts 52	0.33	0.35	0.62	0.56	0.74	0.53	0.60	0.83	0.41	0.93	0.58
MLD 18	0.67	0.50	0.46	0.42	0.62	0.38	0.44	0.54	0.50	0.92	0.67
MLD 40	0.89	0.81	0.69	0.67	0.56	0.77	0.50	0.75	0.77	0.73	1.00
LH 4	0.50	0.40	0.37	0.37	0.53	0.35	0.60	0.75	0.35	0.60	0.72
AL 128	0.25	0.47	0.38	0.53	0.47	0.50	0.33	0.50	0.33	0.60	0.69
AL 198	0.44	0.65	0.47	0.50	0.53	0.50	0.62	0.75	0.67	0.58	0.87
AL 266	0.62	0.41	0.69	0.54	0.81	0.44	0.80	0.70	0.47	0.64	0.73
AL 277	0.67	0.71	0.79	0.69	0.64	0.33	0.80	0.80	0.54	0.44	0.67
AL 288	0.75	0.44	0.57	0.47	0.59	0.23	0.40	0.50	0.35	0.73	0.62
AL 333	0.50	0.62	0.77	0.50	0.62	0.73	0.56	0.56	0.60	0.61	0.86
AL 400	0.58	0.42	0.67	0.56	0.67	0.44	0.80	0.73	0.50	0.64	0.83
H. sapiens	0.50	0.55	0.50	0.56	0.58	0.47	0.60	0.67	0.53	0.67	0.79

TABLE 4.02 [Contd.]

Specimen	Zh.H1	Zh.K1	Sang1	Sang9	Ar.2	Ar.13	Mauer	SK12	SK23	SK34	TM1517
Zh.H1	0.00										
Zh.K1	0.60	0.00									
Sang.1	0.36	0.64	0.00								
Sang.9	0.64	0.85	0.70	0.00							
Arago 2	0.50	0.58	0.31	0.83	0.00						
Arago13	0.67	0.86	0.61	0.54	0.50	0.00					
Mauer	0.50	0.75	0.46	0.31	0.69	0.31	0.00				
SK 12	0.83	1.00	0.54	0.58	1.00	0.67	0.61	0.00			
SK 23	1.25	1.37	1.08	0.75	1.47	0.94	0.95	0.77	0.00		
SK 34	0.82	0.87	0.83	0.47	1.00	0.80	0.63	0.82	0.58	0.00	
TM 1517	0.89	0.69	0.60	0.61	0.91	0.54	0.60	0.67	0.67	0.53	0.00
ER 1482	0.58	0.67	0.46	0.75	0.94	0.71	0.75	0.85	1.07	0.69	0.91
ER 729	1.17	1.44	1.08	0.94	1.50	1.06	1.00	0.92	0.57	0.53	0.67
ER 818	0.75	1.27	0.42	0.64	1.00	0.77	0.61	0.58	1.08	0.75	0.60
ER 3230	1.18	1.33	1.08	0.80	1.53	0.80	1.05	0.92	0.50	0.72	0.57
Peninj	1.00	1.19	1.08	0.56	1.25	0.62	0.77	0.85	0.52	0.63	0.60
Sts 7	0.64	0.75	0.50	0.40	0.92	0.50	0.40	0.33	0.73	0.71	0.50
Sts 36	0.73	0.61	0.70	0.50	1.00	0.69	0.56	0.58	0.87	0.40	0.54
Sts 52	0.92	0.62	0.85	0.56	0.94	0.37	0.54	0.92	0.95	0.68	0.40
MLD 18	0.89	0.85	0.70	0.43	0.83	0.38	0.39	0.60	0.61	0.59	0.57
MLD 40	0.70	1.19	0.82	0.61	1.17	0.86	0.69	0.50	0.56	0.53	0.85
LH 4	0.58	0.87	0.61	0.31	0.87	0.62	0.45	0.85	0.89	0.47	0.67
AL 128	0.67	0.69	0.64	0.42	0.82	0.69	0.33	0.56	0.73	0.43	0.33
AL 198	0.54	0.73	0.67	0.60	0.69	0.87	0.59	0.73	0.94	0.76	0.73
AL 266	0.91	0.85	0.58	0.79	0.53	0.67	0.76	1.08	1.06	0.53	0.61
AL 277	0.50	0.71	0.44	0.36	0.70	0.58	0.36	0.87	0.93	0.38	0.73
AL 288	0.92	0.71	0.77	0.57	1.00	0.50	0.61	0.61	0.65	0.40	0.31
AL 333	0.82	0.92	0.75	0.31	0.64	0.60	0.37	0.83	0.87	0.50	0.67
AL 400	0.82	0.80	0.75	0.27	0.87	0.53	0.48	1.00	0.80	0.33	0.64
H. sapiens	0.42	0.75	0.54	0.37	0.69	0.50	0.32	0.85	1.05	0.63	0.53

TABLE 4.02 [Contd.]

Specimen	ER 1482	ER 729	ER 818	ER 3230	Peninj	Sts 7	Sts36	Sts52	MLD18	MLD40
ER 1482	0.00									
ER 729	1.06	0.00								
ER 818	0.92	0.85	0.00							
ER 3230	1.00	0.43	0.83	0.00						
Peninj	0.94	0.59	0.92	0.43	0.00					
Sts 7	0.67	0.87	0.45	0.79	0.67	0.00				
Sts 36	0.58	0.94	0.54	0.80	0.81	0.33	0.00			
Sts 52	0.75	1.00	1.00	0.90	0.77	0.47	0.56	0.00		
MLD 18	0.67	0.67	0.80	0.65	0.44	0.15	0.43	0.56	0.00	
MLD 40	0.92	0.62	0.73	0.67	0.62	0.50	0.85	0.94	0.69	0.00
LH 4	0.44	0.80	0.61	0.74	0.75	0.47	0.44	0.55	0.50	0.56
AL 128	0.36	0.67	0.60	1.00	0.80	0.27	0.50	0.33	0.42	0.54
AL 198	0.38	0.76	0.92	1.00	0.88	0.43	0.53	0.76	0.47	0.80
AL 266	0.80	0.88	0.83	0.87	0.88	0.92	0.71	0.76	0.71	0.85
AL 277	0.30	1.00	0.89	1.14	0.93	0.50	0.45	0.50	0.45	0.86
AL 288	0.69	0.72	0.85	0.59	0.50	0.38	0.36	0.39	0.29	0.71
AL 333	0.71	0.81	0.92	1.00	0.87	0.58	0.69	0.56	0.46	0.85
AL 400	0.60	0.90	0.92	0.95	0.81	0.57	0.53	0.43	0.53	0.67
H.sap.	0.75	0.95	0.54	0.90	0.73	0.33	0.50	0.59	0.39	0.69

TABLE 4.02 [Contd.]

Specimen	LH 4	AL128	AL198	AL266	AL277	AL288	AL333	AL400
LH 4	0.00							
AL 128	0.33	0.00						
AL 198	0.41	0.36	0.00					
AL 266	0.47	0.50	0.60	0.00				
AL 277	0.43	0.33	0.54	0.54	0.00			
AL 288	0.50	0.31	0.60	0.47	0.50	0.00		
AL 333	0.37	0.38	0.50	0.60	0.42	0.62	0.00	
AL 400	0.26	0.33	0.62	0.44	0.29	0.29	0.31	0.00
H.sap.	0.45	0.47	0.41	0.65	0.50	0.72	0.56	0.71

'Archaic' H. sapiens

Inspection of the character difference matrix (Table 4.01) showed that the Singa cranium was responsible for the single high value of MCD found among the 'archaic' H. sapiens crania. If the Singa cranium is removed from the 'archaic' H. sapiens group the maximum MCD for the group is reduced to 0.66, a value within the intraspecific limits for extant primates. The Singa cranium has some unusual morphological features that have been attributed (in part, and with some reservations) to a pathological condition (Stringer et al., 1985). However, the unusual morphology of Singa is reported as being restricted to aspects of the cranial vault and the sphenoid bone (Stringer et al., 1985). The results of the present study show that Singa does not resemble specimens of H. erectus or modern H. sapiens (Table 4.01). Since the Singa cranium only exhibited a high MCD in one out of four comparisons with other members of 'archaic' H. sapiens it was decided that the specimen could be retained in the latter group.

A. boisei

Of the three possible comparisons between cranial specimens of A. boisei the comparison between ER 732 and OH 5 (MCD = 0.84) exceeded the intraspecific limit of 0.70. If these crania are specifically distinct, then according to the empirical guidelines, ER 406 could either be regarded as belonging in the same species as ER 732 (MCD = 0.67) or it could belong in another species with OH 5 (MCD = 0.60). Rak (1983) has commented on the extent of the morphometric

TABLE 4.03

Mean Character Difference between specimens within conventional hominid taxonomic groups

(for composition of groups, see Table 3.01)

TAXON	CRANIA				MANDIBLES			
	n	Mean	Minimum	Maximum	n	Mean	Minimum	Maximum
H. habilis/ 'early' Homo	7	0.67	0.21	1.20	11	0.61	0.20	1.33*
H. erectus (African)	4	0.49	0.36	0.61	-	-	-	-
H. erectus (Asian)	1	-	-	-	4	0.63	0.36	0.85
H. sapiens (archaic)	5	0.56	0.38	0.82	3	0.50	0.31	0.69
A. afarensis	1	-	-	-	8	0.44	0.26	0.62
A. africanus	2	0.56	0.56	0.56	5	0.55	0.15	0.94
A. robustus	4	0.49	0.40	0.62	4	0.67	0.53	0.82
A. boisei	3	0.70	0.60	0.84	5	0.80	0.43	1.06

* Sample of mandibles for H. habilis/'early' Homo may also include some mandibles of African H. erectus.

difference between ER 732 and the 'male' A. boisei crania: "Such a large discrepancy between the facial indices of male and female does not even exist in species characterised by considerable sexual dimorphism, such as the gorilla" (Rak, 1983, p. 55). Rak (1983) has, however, identified several non-metric characters which appear to be common to OH 5, ER 406 and ER 732, and he considers all three specimens to be conspecific. Other workers have reported that morphometric differences between ER 406, ER 732 and OH 5 are consistent, *in* pattern and degree, with the intraspecific variation found in extant hominoids (Corruccini, 1976; Wood, 1985b).

Rak (1983) commented further on the facial morphology of ER 732: "the indices and some facial elements of the female A. boisei specimen KNM-ER 732 are much closer to what characterises A. robustus than are those of the A. boisei males" (Rak, 1983, p. 122). Inspection of the character difference matrix (Table 4.01) shows that ER 732 is indeed close to A. robustus (MCD = 0.40, average of four comparisons). However, in this study ER 732 also appears to be as similar to the crania of A. africanus, Sts 5 and Sts 71 (MCD = 0.40 and 0.50 respectively). ER 732 is therefore, at least initially, best regarded as a specimen of unknown affinities, and it is excluded from the hypodigm of A. boisei for the purposes of the present analysis.

Among the five mandibles conventionally attributed to A. boisei the empirical maximum MCD of 0.9 was exceeded in all comparisons involving ER 1482. This mandible has been referred to A. boisei by White (1977) and Howell (1978), but other workers have recognised that the specimen differs from typical 'robust' australopithecine mandibles (R.E.F. Leakey, 1976a; Wood, 1976a; Walker and Leakey, 1978). Recent studies of dental enamel thickness and structure (Beynon and Wood, 1986) and of mandibular postcanine tooth root morphology (Wood *et al.*, in press) provide evidence that ER 1482 represents a more primitive hominid than *A. boisei*. Inspection of the character difference matrix suggests that ER 1482 has closest affinities with eight mandibles attributed to *A. afarensis* (MCD = 0.54, average of eight comparisons). Removal of ER 1482 from *A. boisei* (which is advocated here) leaves four mandibles representing that species: ER 729, ER 818, ER 3230 and Peninj. This mandibular sample is regarded as exhibiting a tolerable degree of variation for a fossil hominid species (average MCD = 0.68, maximum MCD = 0.92).

A. africanus

The five mandibles attributed to *A. africanus* include two from Makapansgat, MLD 18 and MLD 40. Inspection of the character difference matrix shows that it is the comparison between Sts 52 and MLD 40 that yields the maximum value of MCD = 0.94 for these mandibles. Several authors, including Tobias (1967, 1973a, 1973b, 1980c), Aguirre (1970), Wallace (1975) and Krantz (1977), have suggested that the Makapansgat hominids are more 'robust' than those found at Sterkfontein. The character difference matrix (Table 4.02) shows that the Makapansgat mandibles could indeed be combined with the four mandibles of *A. robustus* to form a single group, without exceeding the empirically-determined limit for intraspecific variation. Nonetheless, according to the character difference matrix, MLD 18 shows closer affinities to the Sterkfontein mandibles than to the South African 'robust' mandibles. Since only one comparison, involving MLD 40, is at variance with the conventional grouping of *A. africanus* mandibles, specimens in this taxonomic category have not been reallocated.

H. habilis/'early' *Homo*

The highest within-group values of MCD for any of the conventional groups of fossil hominids are found among the crania and mandibles of *H. habilis*/'early' *Homo*. Among the crania belonging to this category just two specimens, OH 13 and OH 24, are responsible for comparisons with an MCD greater than 0.70. These two crania appear quite similar to each other (MCD = 0.21) yet they are distinct at the species level from most of the other crania in their group (MCD = 0.84, average of 10 comparisons). When OH 13 and OH 24 are removed from the *H. habilis*/ 'early' *Homo* category the remaining crania fall within the limits of a single species (average MCD = 0.54, maximum MCD = 0.69).

Comparisons among the mandibles of *H. habilis*/'early *Homo* are complicated by the possible presence of the taxon 'African' *H. erectus* among these specimens. Nonetheless, the distinctiveness of the Olduvai specimens, observed among the crania of *H. habilis*/ 'early' *Homo*, is also seen among the mandibles in this category. The Olduvai mandibles OH 7, OH 13 and OH 22 are similar to each other (average MCD = 0.26, maximum MCD = 0.37) yet they are distinct, sometimes at the species level, from other specimens in their group (average MCD = 0.70, from 24 pairwise comparisons).

OH 22 has been referred (Howell, 1978; Rightmire, 1980) or compared (M.D. Leakey, 1969; M.D. Leakey, 1978; Day, 1986b) to the species *H. erectus*. However, Rightmire (1980) noted morphological differences between this specimen and other African and Asian mandibles attributed to *H. erectus*. According to Rightmire, the most important features in which OH 22 differed from mandibles of *H. erectus* were the more robust corpus, complete absence of mentum osseum or a mental trigone, well-developed alveolar planum with midline hollowing, strongly developed superior transverse torus and mesiodistally elongated premolars with an oblique orientation of the P_3 crown. Rightmire nonetheless agreed with Howell (1978) in referring OH 22 to *H. erectus*, and suggested that the differences between OH 22 and the rest of the *H. erectus* sample were consistent with intraspecific variation. Rightmire did not, however, compare OH 22 with OH 7, and his comparison between OH 22 and OH 13 was cursory, and ignored the dentition. The diagnosis of *H. habilis* (L.S.B. Leakey *et al.*, 1964) shows that some, if not all, of the morphological differences that Rightmire found between OH 22 and *H. erectus* are points of resemblance between OH 22 and *H. habilis*. Such resemblance is confirmed by the results of this study which show that OH 22 is more similar to OH 7 and OH 13 than it is to Asian mandibles of *H. erectus*. Accordingly, OH 22 is referred to *H. habilis* for the purposes of this study.

When the three Olduvai specimens are removed from the *H. habilis*/ 'early' *Homo* category the eight remaining mandibles still exhibit a large range of shape variation (average MCD = 0.57, Maximum MCD = 1.10). It might be expected that some of the heterogeneity in these remaining mandibles is due to the presence of specimens of 'African' *H. erectus*. However, inspection of the character difference matrix shows that the remaining 'early' *Homo* mandibles cannot be separated unequivocally into further categories on the basis of morphological comparisons between them. Comparison between the African mandibles and the four 'Asian' *H. erectus* mandibles also provides no clear indication of which of the African mandibles might belong to *H. erectus*. However, it can be argued that the mandible of ER 1805 is unlikely to represent the 'African' *H. erectus* category, since the cranium of ER 1805 is unlike the crania of 'African' *H. erectus* (average MCD = 0.77, from four comparisons of the crania). Perhaps the best candidate for an 'African' *H. erectus* mandible is ER 730, which is associated with cranial fragments which are reported to have points of similarity with the crania of 'African' *H. erectus* (R.E.F. Leakey and Walker, 1985). Although the mandibles of ER 730 and ER 1805 appear similar in this analysis, ER 730 appears slightly closer morphologically to the mandibles of 'Asian' *H. erectus* (average MCD = 0.57) than does ER 1805 (MCD = 0.76).

If they do indeed represent different taxa, the fact that the mandibles ER 730 and ER 1805 appear morphologically similar is an indication of the difficulty in distinguishing hominid taxa on the basis of mandibular morphology alone (cf. Tobias, 1973c; Wood and Van Noten, 1986). Since no mandible can unequivocally be assigned to 'African' *H. erectus*, it was decided that apart from the Olduvai mandibles (*H. habilis*) and ER 1805 (*Homo sp.*) the remaining 'early'

Homo mandibles would be placed *incertae sedis*.

Summary of reassignment of specimens

The composition of two conventional taxonomic categories were changed after making within-group comparisons between individual specimens. The range of variation in *A. boisei* was reduced by removing ER 732 (cranium) and ER 1482 (mandible) from this taxonomic category: both specimens were placed *incertae sedis* for the purposes of this study. The category *H. habilis*/'early' *Homo* was subdivided to form *H. habilis* (sensu stricto) and *Homo sp.* All mandibles of *H. habilis*/'early' *Homo*, other than OH 7, OH 13, OH 22 and ER 1805 were placed *incertae sedis*. The composition of the revised taxonomic groups is given in Table 4.04, and the means and ranges of Mean Character Difference in the revised groups are given in Table 4.05.

4.1.2 Between-group shape variation

Comparisons were made between the revised taxonomic groups, again using Mean Character Difference (MCD) as the measure of shape difference. The between-groups comparisons were carried out in two ways. Pairwise comparisons between specimens from different groups were made by extracting the appropriate values from the matrices of pairwise differences between specimens (Tables 4.01 and 4.02). Comparisons between groups were also undertaken after calculating a set of average character states for each group. To increase the accuracy of these latter calculations, the transformed (i.e.

TABLE 4.04

Revised taxonomic groups of fossil hominids

TAXON	CRANIA	MANDIBLES
Homo habilis	OH 13, OH 24	OH 7, OH 13, OH 22
Homo sp.	ER 1470, ER 1805, ER 1813, SK 847, Stw 53	ER 1805
Homo erectus (African)	ER 3733, ER 3883, Ndutu, OH 9	-
Homo erectus (Asian)	Sangiran 4	Sangiran 1, Sangiran 9, Zh.H1, Zh.K1
Homo sapiens (archaic)	Arago, Bodo, Kabwe, Petralona, Singa	Arago 2, Arago 13, Mauer
A. afarensis	AL 200-1, 333-1, 333-45 (Composite Cranium)	LH 4, AL 128, AL 198, AL 266, AL 277, AL 288, AL 333w-60, AL 400
A. africanus	Sts 5, Sts 71	Sts 7, Sts 36, Sts 52, MLD 18, MLD 40
A. robustus	SK 46, SK 48, SK 52, TM 1517	SK 12, SK 23, SK 34, TM 1517
A. boisei	ER 406, OH 5	ER 729, ER 818, ER 3230, Peninj

TABLE 4.05

Mean Character Difference between specimens in revised taxonomic groups

(for composition of revised groups, see Table 4.04; data for unchanged groups is given in Table 4.03).

TAXON	CRANIA				MANDIBLES			
	n	Mean	Minimum	Maximum	n	Mean	Minimum	Maximum
Homo habilis	2	0.21	0.21	0.21	3	0.26	0.20	0.37
Homo sp.	5	0.54	0.27	0.69	1	-	-	-
A. boisei	2	0.60	0.60	0.60	4	0.68	0.43	0.92

size-standardised) data for the specimens in each group were averaged prior to calculating the character states for that group. It should be noted that the former type of comparison, between individual specimens, conflates two different sources of variation: both intraspecific and interspecific variation contribute to the difference established by such comparisons. The effect of making comparisons between group averages will generally be to reduce the maximum observed level of variation, but will also depend on the statistical relationship between intraspecific and interspecific variation.

Pairwise comparisons between specimens from different groups.

The purpose of making pairwise comparisons between specimens from different groups was to investigate the possibility that some groups might represent different populations of the same species. Tobias (1980c) proposed that *A. afarensis* and *A. africanus* might be conspecific, and Johanson and White (1979 (but see White *et al*., 1981)) have treated *A. robustus* and *A. boisei* as a single species. Most authors regard the African and Asian samples of *H. erectus* as belonging to the same species (but see Andrews, 1984, for a review of the case for taxonomic subdivision of this species). Stringer (1984) has suggested that the group referred to here as 'archaic' *H. sapiens* may be a distinct species in its own right.

A. africanus and *A. afarensis*

The comparison between the 'composite' cranium of *A. afarensis* and two crania of *A. africanus* suggests that these species are distinct at the species level (MCD = 1.00 and 0.85 for comparisons involving Sts 5 and Sts 71 respectively). The validity of these comparisons depends on accepting that the specimens combined in the reconstruction of the composite *A. afarensis* cranium are from individuals of similar size and shape. This assumption receives indirect support from the relatively narrow range of shape variation among the mandibles of *A. afarensis* (see Table 4.02), and is further supported by the metrical similarity between elements common to two of the specimens incorporated in the composite reconstruction (see data in Kimbel *et al*., 1984).

Although the crania of *A. africanus* and *A. afarensis* appear to be distinct, the mandibles of these species are quite similar. Comparisons between mandibles of the two species give Mean Character Differences within the limits of variation of a single species (mean MCD = 0.56, maximum MCD = 0.92, for 40 comparisons between *A. africanus* and *A. afarensis*). Indeed, the combined sample of mandibles from these two species appears to be no more variable than the sample of five *A. africanus* mandibles alone (mean MCD = 0.55, maximum MCD = 0.94 for 10 comparisons among *A. africanus*).

A. robustus and *A. boisei*

After excluding ER 732 from *A. boisei*, the remaining crania (ER 406 and OH 5) are nonetheless as different from each other (MCD = 0.60) as they are from the crania of *A. robustus* (mean MCD = 0.60, maximum MCD = 0.75 for eight comparisons between the two species).

Tattersall and Eldredge (1977) suggested that ER 406 was intermediate, in cranio-facial morphology, between A. robustus and the holotype of A. boisei, OH 5. My data do not support this suggestion: in fact, OH 5 is marginally more similar to A. robustus (MCD = 0.57) than is ER 406 (MCD = 0.62). Comparisons between the mandibles of A. robustus and A. boisei show that the average difference between the species (mean MCD = 0.69, maximum MCD = 1.08 for 16 comparisons among mandibles) is comparable with the average differences found within each species.

Taken together, these results suggest that there is no clear morphological distinction between material attributed to A. robustus and A. boisei. Nonetheless, the aggregation of these categories would create a sample in which both the cranial and the mandibular variation would exceed the empirically-determined limit for within-species variation. There are, moreover, marked size differences between these taxa (White et al., 1981; see also Section 4.2 below). It seems prudent to maintain, as a working hypothesis, a species distinction between the South and East African 'robust' hominids, particularly in the light of discoveries of further 'robust' forms at West Turkana (Walker et al., 1986).

H. erectus

Comparisons of Sangiran 4 (the single cranium of Asian H. erectus analysed in this study) with crania of African H. erectus gave a mean MCD of 0.60 and a maximum MCD of 0.75. There is no marked distinction betwen these two taxonomic categories, but the inclusion of the Asian specimen along with the African specimens as a single sample is unwarranted, if the limit for intraspecific variation is to be respected.

H. sapiens

The crania of 'archaic' H. sapiens are quite distinct from the single cranium of Asian H. erectus (average MCD = 0.80, maximum MCD = 0.95, from 5 comparisons) and from the African H. erectus sample (average MCD = 0.80, maximum = 1.07, from 20 comparisons). The 'archaic' H. sapiens crania, as would be expected, are closer to the average of 20 modern H. sapiens crania (average MCD = 0.63, maximum MCD = 0.85). There are no distinctions at the species level among mandibles from all three taxonomic categories (Table 4.02).

Pairwise comparisons between group averages

Table 4.06 gives the matrix of MCDs for pairwise comparisons between 'average' primate crania. These values were computed in the following way. Raw measurements for individual primate crania were corrected for size variation using Kazmierczak's transformation. For the sample of 20 crania of each taxon in turn, the transformed data for each character were averaged, and these averages were then converted into character states. The values of MCD between these 'average' primate crania generally fall within the range of interspecific values of MCD obtained when individual crania from different primate species were compared (see subsection 3.3.3 and Figures 3.10 and 3.11 above). It should be noted that the

TABLE 4.06

Matrix of values of MCD between 'average' extant primate species

These values are based on species averages: character states were calculated for each species after averaging the size-corrected data for individual specimens.

TAXON	Pan	Gorilla	Pongo	Hylob.	Colobus	Papio
Pan	0.00					
Gorilla	0.43	0.00				
Pongo	0.53	0.57	0.00			
Hylobates	0.84	0.97	1.28	0.00		
Colobus	0.63	0.74	0.96	0.85	0.00	
Papio	0.87	0.76	0.84	1.47	0.97	0.00
Homo	1.26	1.49	1.68	1.10	1.34	1.96

TABLE 4.07

Matrix of values of MCD between 'average' hominid species

(Values were calculated as for Table 4.06)

Taxon	H.hab.	H.sp.	H.erec. (African)	H.erec (Asian)	A.rob	A.boi	A.afa	A.afr	H.sap. (archaic)
H. habilis	0.00								
H. species	0.61	0.00							
H. erectus (African)	0.38	0.58	0.00						
H. erectus (Asian)	0.55	0.63	0.52	0.00					
A. robustus	0.71	0.45	0.94	0.96	0.00				
A. boisei	0.91	0.71	0.98	1.21	0.48	0.00			
A. afarensis	0.63	0.78	0.89	1.00	0.69	0.78	0.00		
A. africanus	0.58	0.49	0.60	0.75	0.55	0.70	0.85	0.00	
H. sapiens (archaic)	0.76	0.86	0.71	0.79	1.09	1.31	1.17	0.94	0.00
H. sapiens (modern)	0.91	0.92	0.93	1.03	1.02	1.37	1.00	1.12	0.49

comparisons between group averages are based on the complete data set of 90 characters, whereas the results for comparisons between individuals were reported separately for the cranial and mandibular data sets.

In Table 4.07 the matrix of pairwise comparisons between the hominid taxa is given, calculated as indicated above for the primate taxa. The values of MCD in the two tables are broadly comparable. For example, the MCD between A. boisei and A. robustus (0.48) is comparable to the smallest MCD found between the group averages for extant primate taxa (MCD = 0.43, for the comparison between Pan and Gorilla). The numbers of specimens in the hominid samples are, however, much smaller than the samples of 20 crania obtained for each primate taxon.

The values of MCD given in Table 4.07 indicate that the average phenetic affinities of H. habilis lie with African and Asian samples of H. erectus, while Homo sp. has its closest affinities with A. robustus and A. africanus. This interesting pattern of relationships is explored further in the following chapter.

4.2 Comparison by overall size

4.2.1 Within-group size variation

In Chapter 3 it was shown that k is a logarithmic measure of the overall size of a specimen relative to the size of the 'standard' primate. Since k is a proportional measure of size, the range of values of k within groups can be compared across groups, in much the same way that the coefficient of variation can be used to compare variation in groups which have different mean values. The maximum ranges of k for balanced-sex samples of seven extant primate taxa were extracted from Table 3.09 and are given in Table 4.08. Papio, which in terms of the overall size of the skull is the most dimorphic of these primates (Table 3.08), is also the taxon which exhibits the widest range of intraspecific variation in k, for both the cranium and the mandible (Table 4.08).

The ranges of variation in k for the fossil hominid groups are given in Table 4.09, and the values of k for individual hominid specimens are listed in Table 4.10. Table 4.09 shows that the crania of H. sp. and the mandibles of A. boisei exhibit extreme variation in size when compared to the size variation seen in extant primate species (Table 4.08). The five crania of H. sp. are as variable in size as the sample of 10 Papio crania, while the A. boisei mandibles are more variable in size than those of Papio. Size variation among the mandibles of 'Asian' H. erectus, and among those of A. afarensis, is also quite marked.

TABLE 4.08

Range of variation in k (logarithmic relative size) in balanced-sex samples of extant primates species

Taxon	Crania	Mandibles
Pan	.047	.051
Pongo	.080	.077
Gorilla	.056	.067
Homo	.044	.037
Hylobates	.038	.059
Papio	.100	.143
Colobus	.047	.060

Data are taken from Table 3.09. The sample for each taxon comprises five individuals of each sex. The range of variation in k for a given taxon is equal to the log of the ratio of the overall size of the largest specimen to the overall size of the smallest specimen.

A. afarensis

The proposers of A. afarensis emphasised that the skeletal remains of this species vary markedly in size yet are similar in shape (Johanson et al., 1978a). My mandibular data for this species confirm these observations, since there is little shape variation (Table 4.03) yet appreciable size variation among these specimens (Table 4.09). This corresponds with the pattern seen among the extant primate species, where taxa that vary more in size (Table 4.08; Figures 3.11 and 3.12) are not necessarily more variable in shape (Figures 3.09 and 3.10).

Evidence for size variation in A. afarensis has also been found in the postcranial remains of this species. The average linear size ratio between small and large postcrania of A. afarensis has been estimated by Johanson and White (1979) to be 81%, while data given by McHenry (1986) provide a similar value of 78%. These ratios correspond to a range of k of 0.092 and 0.108 respectively for the variation between small and large postcrania, and these values are in turn comparable with the range of k of 0.104 recorded for the eight mandibles of A. afarensis in this study (Table 4.09).

A. boisei

Chamberlain and Wood (1985) noted that the variation in the cross-sectional area of the mandibles of the 'robust' australopithecines (A. robustus and A. boisei) might indicate that these taxa were strongly sexually dimorphic. The variation in overall size among the A. robustus mandibles considered here is consistent with the size

TABLE 4.09

Range of variation in k (logarithmic relative size) in revised fossil hominid groups (numbers of specimens given in brackets)

Taxon	Crania	Mandibles
H. habilis	0.018 (2)	0.041 (3)
H. sp.	0.101 (5)	-
H. erectus (African)	0.048 (4)	-
H. erectus (Asian)	-	0.102 (4)
H. sapiens (archaic)	0.065 (5)	0.054 (3)
A. africanus	0.007 (2)	0.067 (5)
A. afarensis	-	0.104 (8)
A. robustus	0.042 (4)	0.078 (4)
A. boisei	0.015 (2)	0.162 (4)

range seen in the mandibles of sexually dimorphic large-bodied hominoids (Table 4.08). However, the range in size among the A. boisei mandibles exceeds that of any of the extant primates studied here. A single mandible (ER 818) is responsible for the large size range in A. boisei sample studied here (Table 4.10). This specimen is not only aberrantly large, but also differs markedly in shape from the three other mandibles attributed here to A. boisei (ER 729, ER 3230 and Peninj: see Table 4.02 for shape comparisons). It is possible that ER 818, rather than representing a larger morph of A. boisei (presumed to be the male morph by Chamberlain and Wood, 1985) is in fact attributable to a separate East African 'robust' taxon. It is interesting to note that extreme size variation has also been observed among juvenile mandibles attributed to A. boisei (Dean, personal communication).

The cranial specimen ER 732 was excluded from A. boisei on the grounds of its difference in shape from OH 5 and ER 406. ER 732 is also markedly smaller in overall size than either of the latter two crania. Inclusion of ER 732 in A. boisei would extend the range of cranial size in that species to a level that corresponds with the maximum range of size seen in Papio.

Homo sp.

The five crania attributed to Homo sp. have a size range comparable with Papio, which exhibits the greatest range of cranial size found among the extant taxa included in this study. Nonetheless, the shape variation among these specimens does not appear to exceed the level

TABLE 4.10

Values of k (logarithmic relative size) for individual hominids

Taxonomic Group	Crania	k	Mandibles	k
H. habilis	OH 13	0.086	OH 13	0.018
	OH 24	0.068	OH 7	0.059
			OH 22	0.047
H. sp.	ER 1805	0.073	ER 1805	0.078
	ER 1470	0.113		
	ER 1813	0.021		
	SK 847	0.024		
	Stw 53	0.012		
Homo (sp. indet.)	-		ER 730	0.056
			ER 992	0.070
			ER 1802	0.102
			BK 67	0.066
			BK 8518	0.030
			SK 15	0.037
			ER 3734	0.027
H. erectus (African)	ER 3733	0.118		
	ER 3883	0.122		
	Ndutu	0.135		
	OH 9	0.166		
H. erectus (Asian)	Sang.4	0.121	Sang.1	0.080
			Sang.9	0.059
			Zh. H1	-0.022
			Zh. K1	0.003
H. sapiens (archaic)	Arago	0.108	Arago 2	0.012
	Singa	0.164	Arago 13	0.066
	Petralona	0.130	Mauer	0.030
	Kabwe	0.119		
	Bodo	0.173		
A. africanus	Sts 5	0.042	Sts 7	0.111
	Sts 71	0.035	Sts 36	0.079
			Sts 52	0.052
			MLD 18	0.044
			MLD 40	0.078
A. robustus	TM 1517	0.076	TM 1517	0.095
	SK 46	0.034	SK 12	0.161
	SK 48	0.057	SK 23	0.083
	SK 52	0.075	SK 34	0.084

TABLE 4.10 [Contd.]

Taxonomic Group	Crania	k	Mandibles	k
A. boisei	OH 5	0.103	Peninj	0.105
	ER 406	0.118	ER 729	0.166
			ER 818	0.267
			ER 3230	0.152
Australopithecus (sp. indet.)	ER 732	0.022	ER 1482	0.104
A. afarensis	Composite	0.076	LH 4	0.073
			AL 128	0.013
			AL 198	0.036
			AL 266	0.063
			AL 277	0.068
			AL 288	0.009
			AL 333	0.113
			AL 400	0.057

Note: k is equal to the log of the ratio of the overall size of the specimen to the overall size of the 'standard', or average, primate.

found within extant primates (Table 4.01). Apart from ER 1805, the mandibles belonging to this taxonomic category are not known with certainty (Table 4.10). However, the range of variation among the unclassified Homo mandibles (belonging either to Homo sp. or to Homo erectus) is comparable with the size range seen within dimorphic primate species.

Within fossil hominid groups there is a tendency for the mandibles to be more variable in size than the cranial samples for the same groups (Table 4.09). This phenomenon might be attributable to the larger samples of mandibles compared to the smaller number of cranial remains. Nonetheless, among the extant primate samples, which comprised equal numbers of crania and mandibles, there is also a tendency for mandibles to vary in size more than crania (Table 4.08). Mandibular size values are based on fewer variables than cranial size values, and the effects of such factors as allometry and sexual dimorphism may be more noticeable when attention is confined to the mandible.

4.2.2 Between-group size variation

As with the shape comparisons, the between-group variation in size can be examined either between individuals of different groups or between group averages. Inspection of the individual values of k for fossil hominids (Table 4.10) shows that the H. habilis crania fall within the extensive size range of the crania of Homo sp., but crania of both taxa are smaller than those of H. erectus or 'archaic'

H. sapiens. Mandibles of the early species of Homo, however, are comparable in size to those of the later species. Among the australopithecines, A. boisei is noticeably larger in size than A. robustus, although the distributions of mandibular size in these species overlap. A. robustus, on the other hand, is rather closer in size to A. africanus. The large morph of A. afarensis is comparable in size both with A. robustus and with the larger specimens of A. africanus, but the smallest mandibles of A. afarensis are appreciably smaller than the mandibles of the other australopithecine species.

The average values of k for the fossil hominid groups are listed separately for crania and mandibles in Table 4.11 (the same data are presented graphically in Figure 4.01). These values were obtained by averaging the values for individual specimens. For comparison, the average values for k for the extant primate taxa have been extracted from Table 3.09 and are listed in Table 4.12. Since there is considerable size variation in some of the hominid groups, while in other groups the numbers of specimens is very small, the estimates given in Table 4.11 are less reliable than those obtained for the extant primates. The primate averages, on the other hand, are based on ten complete specimens for each group, with mandibles and crania belonging to the same sample of individuals. The average value of k for the A. afarensis mandibles is given separately for the large morphs of this taxon. The single cranial value is for the reconstructed cranium, which is a composite of large individuals, judged to be males by Kimbel et al. (1984), and its size corresponds to that of the large mandible, AL 333w-60, which Kimbel et al. (1984)

TABLE 4.11

Average values of k (logarithmic relative size) in hominid species

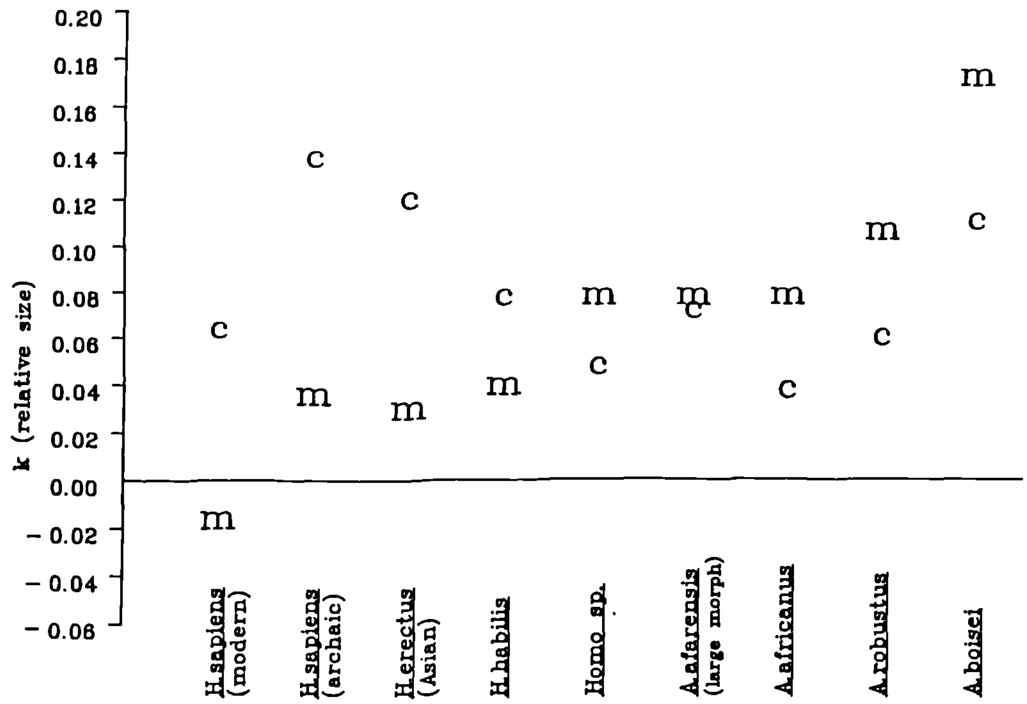
(numbers of specimens in each category are given in parentheses)

Taxonomic Group	Crania	Mandibles
H. habilis	0.077 (2)	0.041 (3)
H. sp.	0.049 (5)	0.078 (1)
H. erectus (African)	0.135 (4)	-
H. erectus (Asian)	0.121 (1)	0.030 (4)
H. sapiens (archaic)	0.138 (5)	0.036 (3)
A. africanus	0.038 (2)	0.072 (5)
A. robustus	0.060 (4)	0.106 (4)
A. boisei	0.110 (2)	0.172 (4)
A. afarensis	0.076[1] (1)	0.075[1] (5) 0.054[2] (8)

1. Large morph of *A. afarensis* (mandibles included are LH 4, AL 266, AL 277, AL 333, AL 400).

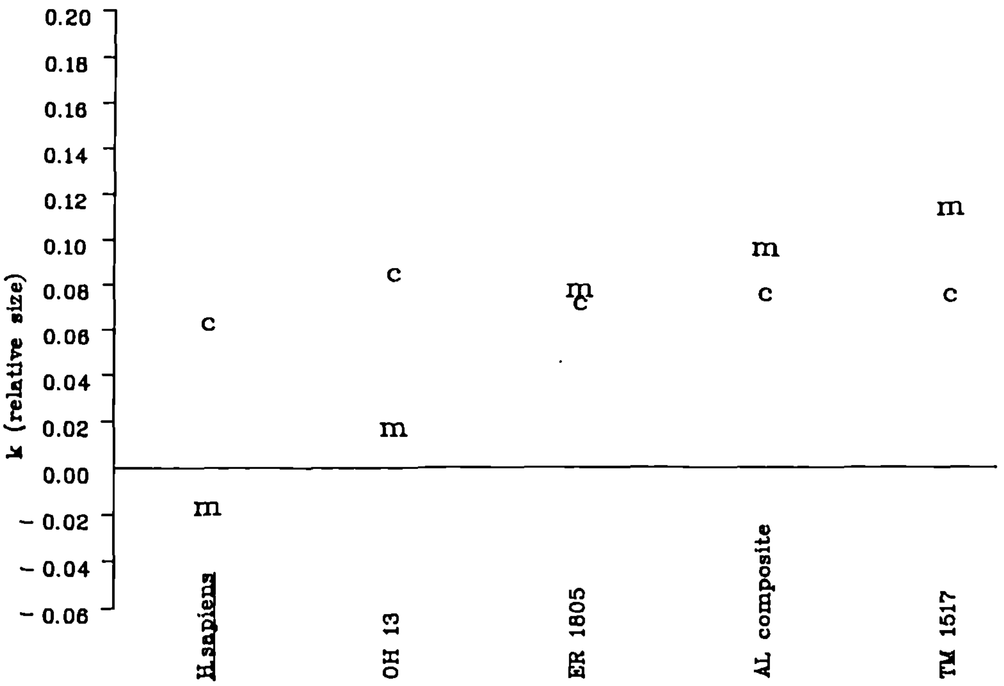
2. All *A. afarensis* mandibles.

Figure 4.01 Average values of k in hominid groups



c = average cranial size m = average mandibular size

Figure 4.02 Values of k in individual hominids in which both cranium and mandible are present



c = cranial size m = mandibular size

TABLE 4.12

Average values of k (logarithmic relative size) in extant primates

(data have been extracted from Table 3.09)

Taxonomic Group	Crania	Mandibles
Pan	0.030	0.026
Pongo	0.049	0.099
Gorilla	0.106	0.127
Homo	0.063	-0.016
Hylobates	-0.224	-0.286
Papio	-0.026	0.013
Colobus	-0.201	-0.169

also incorporated in the same reconstruction.

When one compares the size of the mandible relative to the size of the cranium in different hominid taxa an interesting pattern emerges. Inspection of Table 4.11 shows that three of the fossil species of Homo ('archaic' H. sapiens, H. erectus and H. habilis) resemble modern H. sapiens (Table 4.12) in possessing mandibles that are, on average, small compared to those hominids' respective crania. Homo sp., on the other hand, resembles species of Australopithecus, which all have mandibles that are large in relation to their crania (Table 4.11 and Figure 4.01).

In a few cases both cranial and mandibular specimens are available for the same individual fossil hominid. In these instances one can make a more accurate assessment of the size of the mandible and lower dentition in relation to the rest of the skull. Table 4.13 lists specimens in which such a comparison is possible, together with comparable data for modern Homo sapiens, Pan and the 'average primate' (the latter is represented by the zero point on the scale of relative size). These data confirm that Homo sp. (ER 1805) resembles Australopithecus (TM 1517, AL composite) in having a mandible which is large in relation to the overall size of the rest of its skull, whereas H. habilis (OH 13) is more like modern H. sapiens in its possession of a relatively small lower jaw.

Comparison between mandibular and cranial size in early Homo can be pursued further (albeit in a speculative fashion) by considering fossils which have been associated, on anatomical grounds, by other

TABLE 4.13

Comparison of cranial and mandibular values of k (log. relative size) in individuals in which both cranium and mandible are present

	Values of k (relative size)	
Individual	Cranium	Mandible
OH 13	0.086	0.018
ER 1805	0.073	0.078
TM 1517	0.076	0.095
AL composite	0.076	0.113[1]
Homo sapiens[2]	0.063	-0.016
Pan troglodytes[2]	0.030	0.026
'Average primate'	0.000	0.000

1. k-value for AL 333w-60. This specimen was incorporated in the composite reconstruction published by Kimbel *et al.* (1984). Inspection of alveolar tooth row dimensions shows that the mandible and palate in this reconstruction are well matched.

2. Average values for ten individuals (from Table 4.12).

workers. R.E.F. Leakey (1974, see also R.E. Leakey *et al.*, 1978) considered ER 1802 to be conspecific with ER 1470. If ER 1802 represents the size of lower jaw appropriate for the ER 1470 cranium (as has been tentatively affirmed by Stringer, 1986) then ER 1470 would resemble ER 1805 and *Australopithecus* in possessing a lower jaw that was quite large in relation to its cranial size (ER 1470: $k = 0.113$; ER 1802: $k = 0.102$). In discussing the affinities of SK 847, Clarke and Howell (1972, p. 326) stated that "only a mandible of the size, reduced robusticity, and low ascending ramus found in SK 15 could have fitted this specimen", and they supported their statement with the aid of an illustration of the two specimens in articulation. My data indicate that although SK 15 is a mandible of moderate dimensions ($k = 0.037$), it is in fact rather large relative to the SK 847 cranium ($k = 0.024$). These speculative comparisons indicate that both the ER 1470/ER 1802 and the SK 847/SK 15 composites have mandible-cranium size relationships that agree with the pattern seen in *Homo sp.* (ER 1805) but conflict with the pattern of mandibular size reduction that appears to be characteristic of *H. habilis*, *H. erectus* and *H. sapiens*.

4.3 Detailed comparisons between H. habilis and Homo sp.

4.3.1 Comparison of particular characters

The apparent distinction between H. habilis and Homo sp. in 'overall shape' was investigated in more detail by examining the individual values of size-standardised characters in each group. These values have been plotted for each of the five regions of the skull in Figures 4.03 to 4.08. In each Figure the characters have been arranged in the numerical order given in Table 4.14 (see also Appendix 2). The vertical axis indicates the values of the characters after Kazmierczak's transformation (but before conversion into character states). The separate symbols K, O, B and S designate hominids from Koobi Fora, Olduvai Gorge, Baringo (Kapthurin) and South Africa respectively. Abbreviated character definitions are provided in Table 4.14: more detailed definitions are given in Appendix 2.

Cranial base (Figure 4.03)

Of the 16 characters of the base, 12 were measurable on OH 24 but only one on OH 13. The distribution of values for the Olduvai hominids appears to be distinct from that of Homo sp.. Only in one character does the range of values for Homo sp. encompass the value for an Olduvai hominid (out of a possible nine characters where such a distinction can be tested). OH 24 appears to be relatively wide across the anterior basioccipital (characters B3 and B4) but for a suite of characters (B5 to B10) H. habilis has smaller

TABLE 4.14

Abbreviated definitions of morphometric characters

Characters of the base

B1	TP-TP
B2	CC-CC
B3	PA-PA
B4	FO-FO
B5	IS-IS
B6	EG-LM
B7	TP-CC
B8	PA-CC
B9	FO-CC
B10	IS-CC
B11	BS-OS
B12	FM-FM
B13	ZM-ZR
B14	IT-ZY'
B15	OS [IS/IS
B16	BS-SB

Characters of the vault

V1	LA-LA'
V2	MP-MP
V3	BP-BP
V4	PO-PO
V5	GL-OC
V6	NA-BR
V7	BR-LA
V8	BR-PT
V9	LA-OS
V10	NA^BR
V11	LA^OS
V12	VX [F.H.
V13	PX [C.P.

Characters of the face

F1	FT-FT
F2	ZY-ZY
F3	ZM-ZM
F4	IF-IF
F5	EK-EK
F6	EK-DK
F7	DK-DK
F8	NM-NM
F9	PM-PM
F10	NA-AL
F11	IF-P^4B
F12	ZO-P^4B
F13	FT-M^3B
F14	ZM-M^3B
F15	PO-GL
F16	PO-AL
F17	PO-ZM
F18	NA [FT/FT
F19	SS [ZM/ZM

Characters of the mandible

M1	GN-ID
M2	M_1B-BM_1
M3	M_3B-BM_3
M4	FS-GN
M5	MF-BF
M6	CS-CS'
M7	CM_1-CM_1'
M8	C_1L-C_1L
M9	M_2L-M_2L
M10	ID-I_2D
M11	P_3M-P_4D
M12	M_1M-M_3D
M13	I_1 M-D
M14	I_1 B-L
M15	C_1 M-D
M16	C_1 B-L
M17	P_3 M-D
M18	P_3 B-L
M19	M_1 M-D
M20	M_1 B-L
M21	M_3 M-D
M22	M_3 B-L

Characters of the palate

P1	AL [MT/MT
P2	M^2B-M^2B
P3	C^1L-C^1L
P4	M^2L-M^2L
P5	IC [C^1L/C^1L
P6	PD [M^2L/M^2L
P7	AL [C^1L/C^1L
P8	AL-I^2D
P9	P^3M-P^4D
P10	M^1M-M^3D
P11	I^1 M-D
P12	I^1 B-L
P13	C^1 M-D
P14	C^1 B-L
P15	P^3 M-D
P16	P^3 B-L
P17	M^1 M-D
P18	M^1 B-L
P19	M^3 M-D
P20	M^3 B-L

Note: Full definitions of characters are given in Appendix 2.

size-standardised dimensions than Homo sp.. These latter characters are concentrated in the lateral aspect of the basicranium, adjacent to the temporo-mandibular articulation, and some of them may reflect the reduced size of lower jaw that appears to distinguish H. habilis from Homo sp.. The width of the mandibular fossa (B6), which would be expected to correlate closely with the size of the lower jaw, is relatively smaller in both OH 13 and OH 24 than in the Koobi Fora and South African Homo sp..

Cranial Vault (Figure 4.04)

Two characters of the cranial vault substantiate a distinction between H. habilis and Homo sp.. Vault thickness (V1) and parietal sagittal chord (V7) are appreciably smaller in the former species. Vault thickness must be interpreted with caution for several reasons. Firstly, unlike (for example) measurements taken between suture junctions, measurements of the vault thickness in a fossil may be reduced if the specimen has been abraded or has suffered from exfoliation. Secondly, in this study vault thickness is invariably the smallest non-dental measurement, and observer error is therefore a larger proportion of the total measurement. Thirdly, in several of the more complete cranial specimens this measurement could only be taken with a large spreading calliper, with an estimated confidence of ± 1mm. The distinctively thin vault of H. habilis is, however, confirmed by measurements taken on two other specimens that were too incomplete to be included in this metrical study. Both OH 7 and OH 16 (specimens considered by some authors, including Stringer, 1986, to represent a large morph of early Homo) have an absolute cranial

Fig. 4.03 Comparisons of early Homo crania: Base

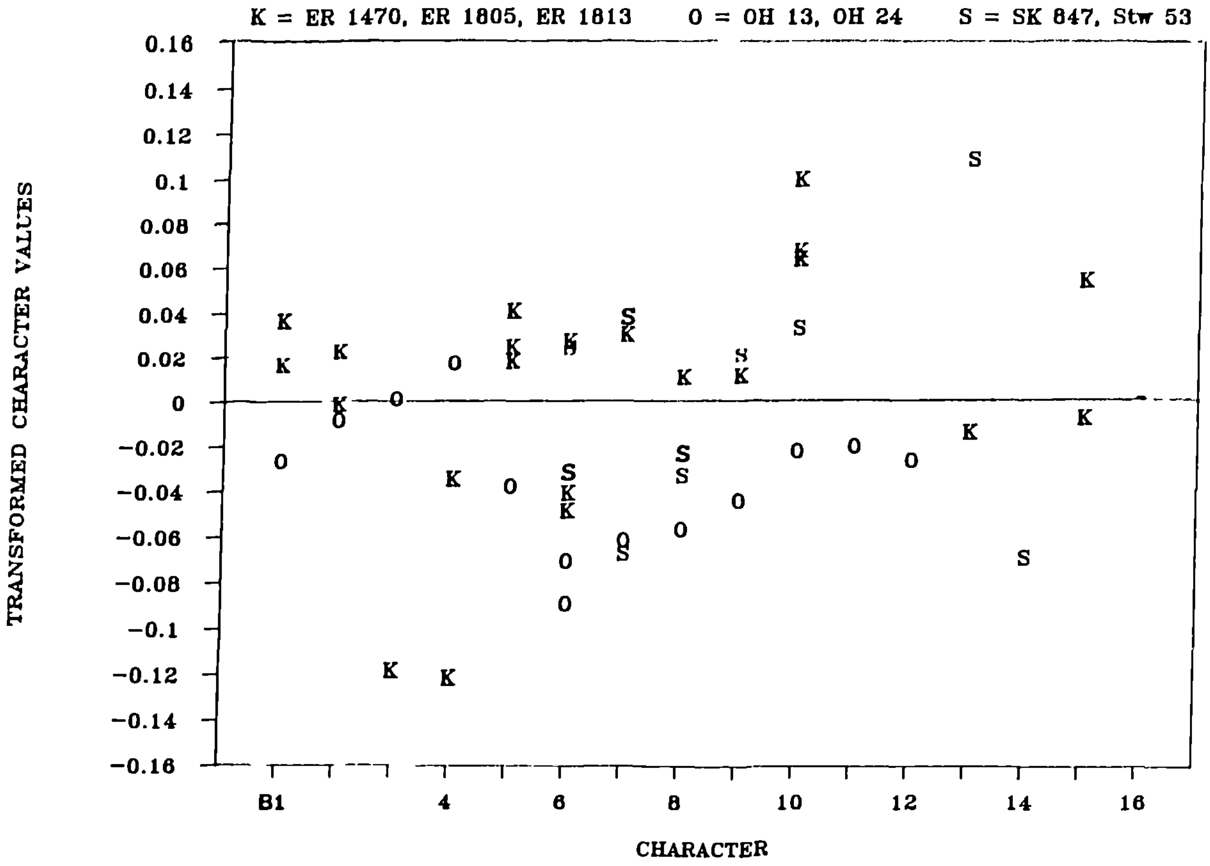
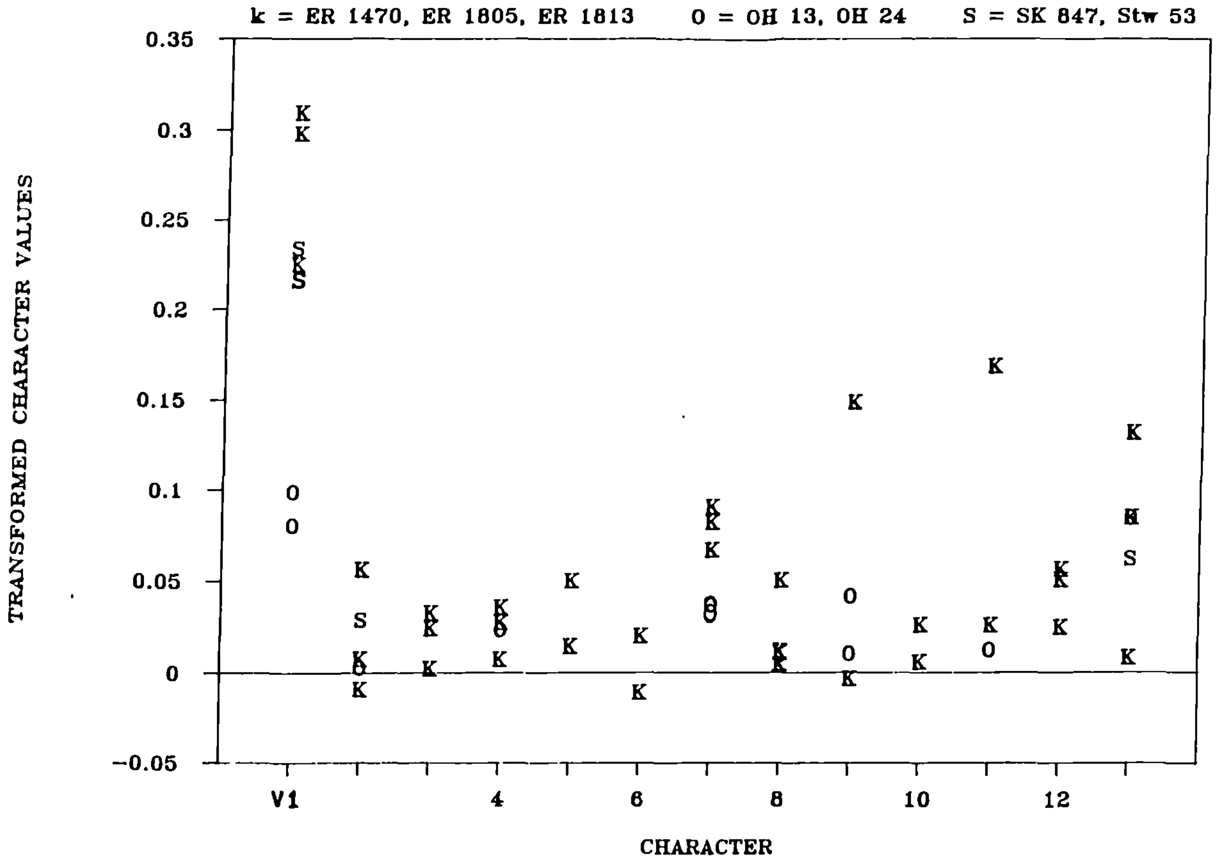


Fig. 4.04 Comparisons of early Homo crania: Vault



vault thickness that is no greater than that of OH 13 or OH 24.

Parietal sagittal dimensions are also potentially subject to error through the presence of accessory bones at bregma and lambda, the landmarks from which these dimensions are measured. Accessory ossicles are extraordinarily common in Plio-Pleistocene hominids. All but one of the Sinanthropus crania possessed an interparietal bone (Weidenreich, 1943, pp. 24-25). The Koobi Fora early hominines ER 1470 and ER 1813 both have numerous lambdoid ossicles, and the latter cranium also possesses an interparietal bone at bregma (Day et al., 1975; Day et al., 1976). ER 730 may have possessed an interparietal bone at lambda: the lambdoid suture in this specimen has no apex in the midline (R.E.F. Leakey and Walker, 1985). A fossilisation defect surrounds the bregmatic area in ER 3733 (R.E.F. Leakey and Walker, 1985), but the margins of this defect indicate that this cranium might also have possessed an accessory bone at bregma. ER 3883 has accessory lambdoid ossicles (R.E.F. Leakey and Walker, 1985).The fragmentary gracile hominid cranium L.894-1, from Member G of the Shungura Formation, may have possessed lambdoid ossicles (Boaz and Howell, 1977). I noted the possible former presence of a large bregmatic ossicle in OH 16 when I examined this specimen: the evidence is seen in the course of sutures in the remaining fragments of this H. habilis cranium. Previous reconstructions of the cranial vault of OH 16 make no allowance for the existence of an accessory bone at bregma, and as a result are probably inaccurate.

The procedure used in the present study to identify bregma and lambda on fossil crania follows the recommendations of Howells (1973) that these points should be defined by the general course of the coronal and lambdoid sutures respectively, at the points where these sutures are intersected by the general course of the sagittal suture. When accessible, cranial radiographs and inspection of the endocranial course of the sutures provided useful additional evidence for the location of these landmarks. As a result, my identifications of lambda on ER 1470 and ER 1813 differ from those of the original describers (Day *et al.*, 1975; Day *et al.*, 1976), who elected to locate this point on the most anterior transverse suture.

Despite the above reservations, a relatively short parietal can be considered to differentiate *H. habilis* from *Homo sp*. It is worthy of note that in an earlier study, employing an independent data set, average parietal sagittal dimensions were also found to be relatively small in the early *Homo* crania, compared to other hominids (Wood and Chamberlain, 1986).

Face (Figure 4.05)

Only one character (F5: biorbital breadth) was measurable in an Olduvai hominid (OH 24). Biorbital breadth is relatively narrow in this specimen, compared to ER 1813, ER 1470 and SK 847. Although Figure 4.05 offers little opportunity for comparing *H. habilis* and *Homo sp.*, it is notable that there is a surprisingly close correspondence between the values of facial characters in ER 1813 and ER 1470 (no facial measurements were obtainable for ER 1805). Other authors (Stringer, 1986; Lieberman, 1986) have dwelt at length on

Fig. 4.05 Comparison of early Homo crania: Face

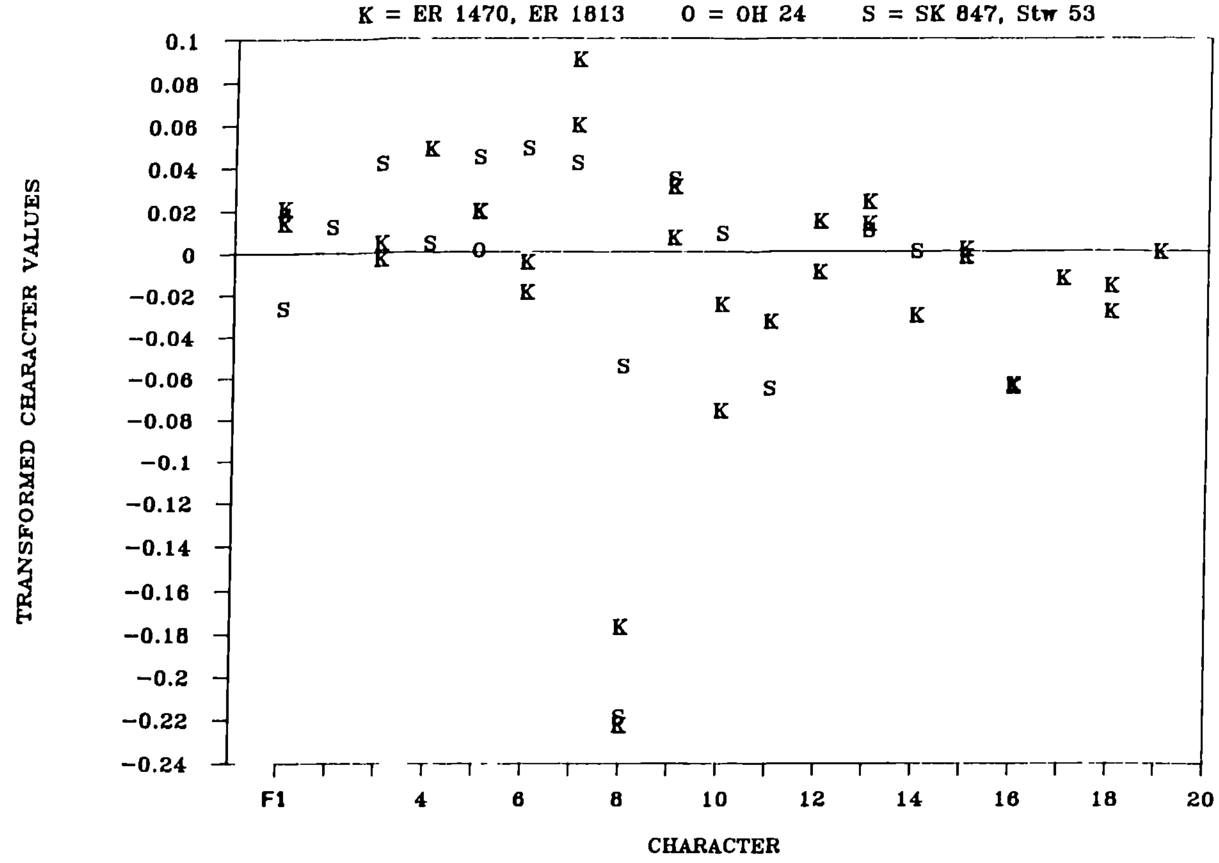
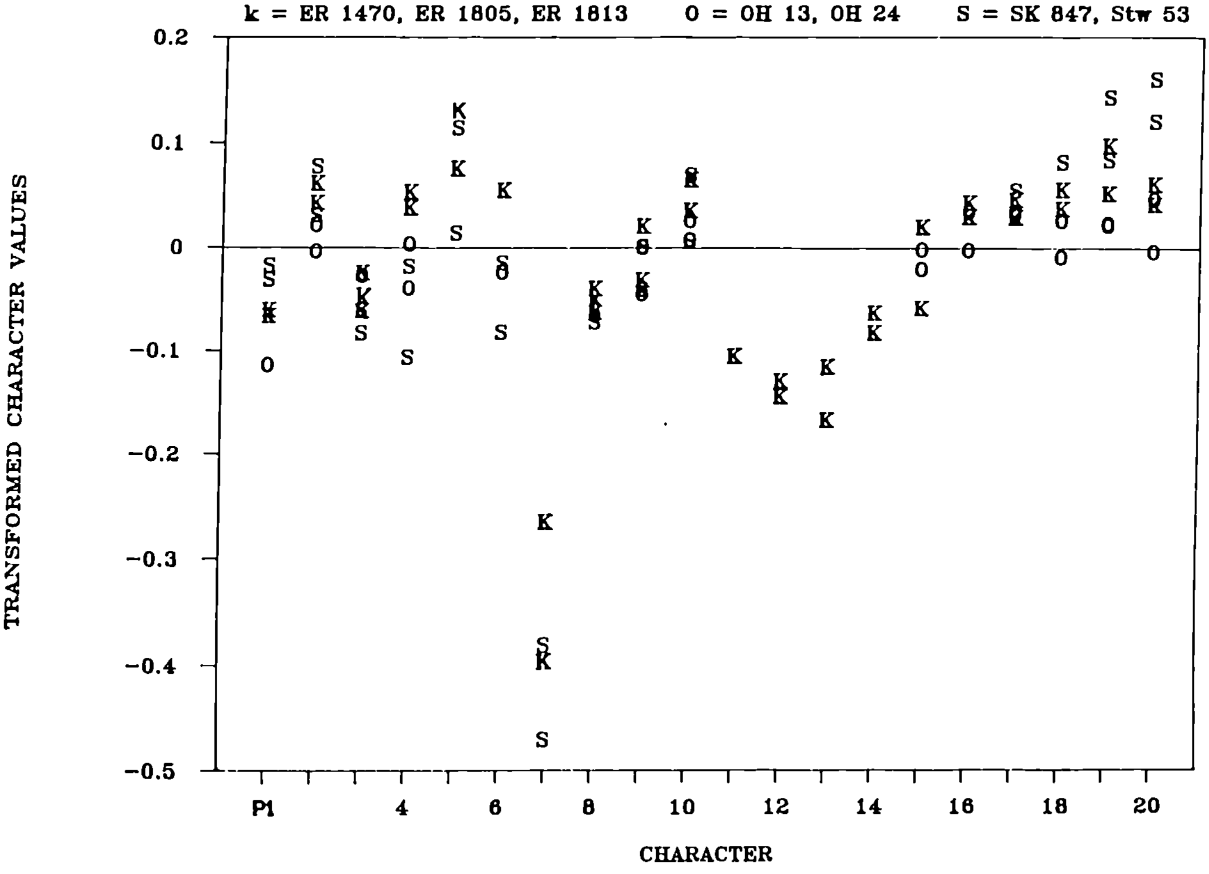


Fig.4.06 Comparison of early Homo crania: Palate



facial differences between ER 1813 and ER 1470. There is little evidence for these differences in my size-adjusted data, although these data do confirm that ER 1813 has a relatively short face compared to ER 1470.

Palate (Figure 4.06)

Palatal characters of *H. habilis* mostly fall within the range of values for *Homo sp.*, but the overall palatal dimensions (P1, P2) and the dimensions of the cheek teeth (P15 to P20) are relatively smaller in *H. habilis*. This is consistent with the earlier finding that the mandible of OH 13 is small in relation to its cranium, since one would expect the upper jaw also to be of reduced size in these hominids.

Mandible (Figures 4.07 and 4.08)

Characters of the mandibular dentition constitute some of the most important elements of the original diagnosis of *H. habilis* (cf. L.S.B. Leakey *et al.*, 1964; see also 2.1.1 above). In particular, large incisors and buccolingual narrowing and mesiodistal elongation of the lower premolars were considered to be diagnostic of this species. In Figures 4.07 and 4.08 the three mandibles considered here to represent *H. habilis* are compared with mandibles tentatively assigned to *Homo sp.* and 'African' *H. erectus* respectively.

There are several characters in which *H. habilis* is distinct from both of the other taxonomic groups. In *H. habilis*, mandibular corpus

Figure 4.07 Comparison of early Homo mandibles (1)

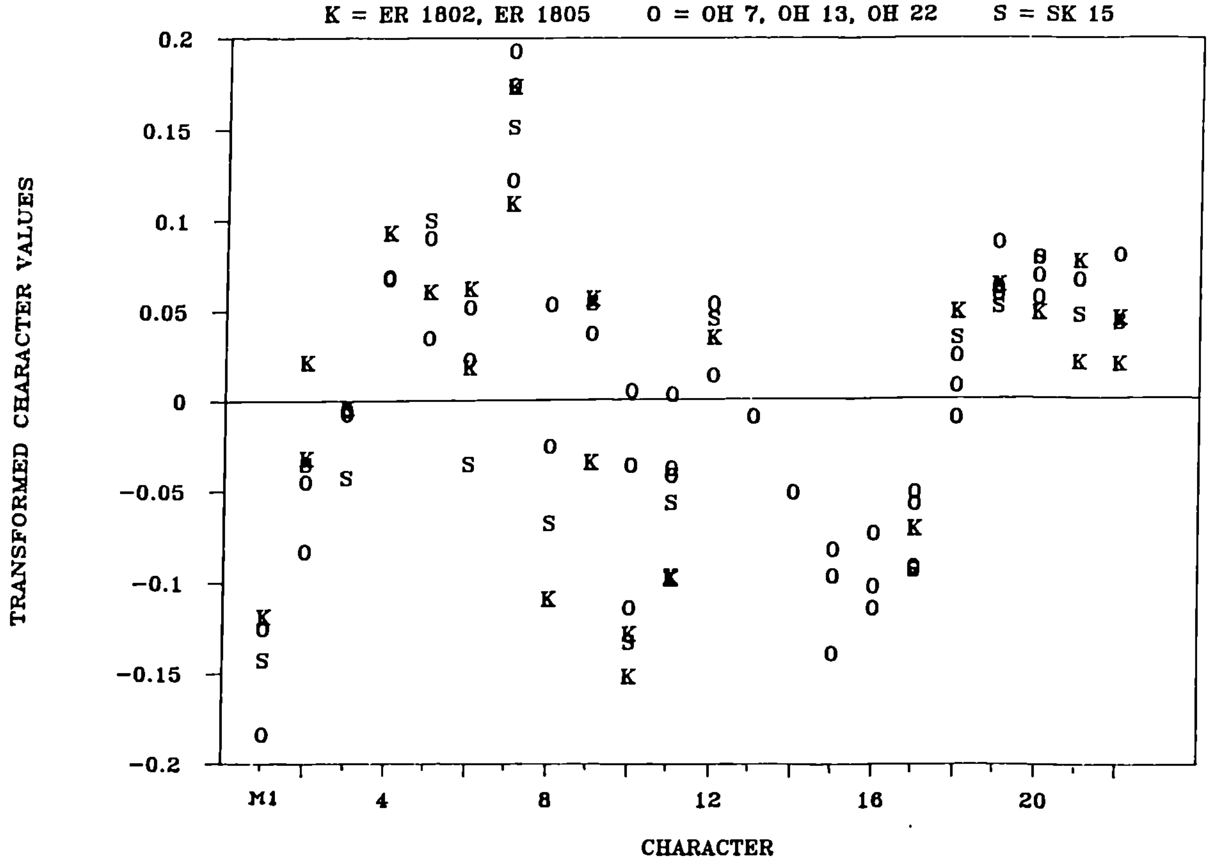
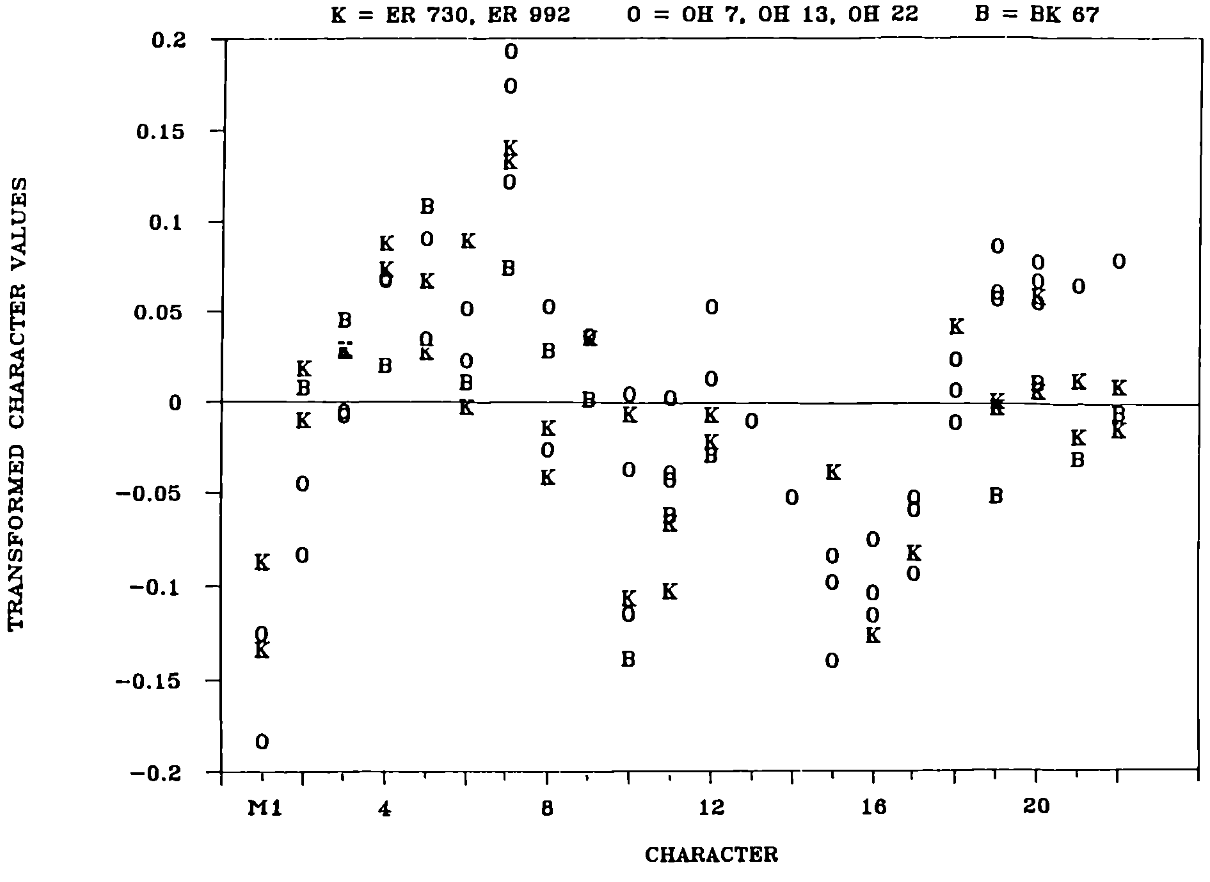


Figure 4.08 Comparison of early Homo mandibles (2)



depth is reduced (M2), premolar alveolar length increased (M11), P_3 buccolingual crown diameter reduced (M18) and most molar dimensions increased (M19 to M22) relative to both Homo sp. and 'African' H. erectus mandibles. Lower incisor dimensions (M13 and M14) are only available for one specimen (OH 7), but two other dimensions also partly reflect the size of the incisors: these are the breadth between the lower canines (M8) and the lower incisor alveolar length (M10). Both dimensions are larger in H. habilis than in Homo sp., but there is substantial overlap in the distribution of characters M8 and M10 in the H. habilis and 'African' H. erectus mandibles.

Summary of differences between H. habilis and Homo sp.

H. habilis appears to be less variable in shape (Table 4.05) and size (Table 4.09) than Homo sp. Even if the latter taxonomic group is restricted to specimens from one site Homo sp. still appears more variable, as evidenced by shape and size differences between ER 1813 and ER 1470 (see Tables 4.01 and 4.10 for individual comparisons of shape and size respectively). The range of size in the three mandibles of H. habilis is comparable with the range of size of samples of mandibles from Pan troglodytes or modern H. sapiens. The size variation in the crania of Homo sp. exceeds that found in Pongo or Gorilla, and is comparable with the size variation seen in Papio. This size variation persists even if only the Koobi Fora crania of Homo sp. are considered.

The overall shape differences between H. habilis and Homo sp., as evidenced by pairwise comparisons between specimens of each taxon, often exceed the empirically-determined limits for intraspecific variation. Therefore, a species-level distinction between the two groups is advocated here. Several characters appear to contribute to the overall shape difference between the two groups. H. habilis has jaws that are relatively small compared to the size of the neurocranium: the mandibular fossa is also relatively smaller in this species. Several characters of the basicranium differ between H. habilis and Homo sp. The cranial vault is relatively thinner and parietal sagittal chord relatively shorter in H. habilis. Characters of the original diagnosis of H. habilis serve to distinguish the mandibular dentition of this species from that of specimens tentatively assigned here to Homo sp. and 'African' H. erectus. Mesiodistal elongation of the cheek teeth, and the possession of relatively large incisors (as inferred from the proportions of the anterior dental arcade) appear to distinguish H. habilis from these other taxa.

4.3.2 Evidence from other studies

A number of morphological studies have been carried out which included specimens of early Homo from both Olduvai Gorge and Koobi Fora. Unfortunately, the samples from these sites have often been combined as a single taxonomic category 'East African early Homo' (EAFHOM). The emphasis of such studies has often been to compare this taxonomic category with other 'gracile' or 'robust' hominid groups. A few studies, however, have either specifically compared the Olduvai Gorge and Koobi Fora gracile hominids, or have provided sufficient data for individual hominids to allow post hoc comparisons to be undertaken.

Groves and Mazak (1975) compared the Olduvai hypodigm of *H. habilis* with gracile hominids from Koobi Fora. They were able to demonstrate (their Figure 2) that the characteristically narrow P_3 of *H. habilis* was not seen among the gracile hominids from Koobi Fora. Several subsequent studies (White *et al.*, 1981; Wood and Abbott, 1983; Stringer, 1986) confirmed that buccolingually narrowed cheek teeth were a feature of EAFHOM, but they did not determine whether there were differences within this category, in particular whether the buccolingual narrowing was confined to the Olduvai material.

Abbott (1984) determined the mandibular premolar root morphology of a large number of Plio-Pleistocene fossil hominids. Her data allow a further distinction to be drawn between *H. habilis* from Olduvai Gorge on the one hand and the Koobi Fora gracile hominids on the other. Specimens of early *Homo* considered by Abbott (1984), together with two additional specimens for which published data are available, are listed in Table 4.15. Of the seven Olduvai hominids for which data are available, six have single-rooted P_3 and P_4 (Table 4.15). In these specimens P_3 usually possesses a Tomes' root, but any bifurcation is confined to the apical third of the root. P_4 may also have a single Tomes' root. One specimen from Bed III at Olduvai Gorge (OH 51) has double-rooted P_3 and P_4 (this specimen has been attributed to *H. erectus* by some authors). The Koobi Fora hominids (here assigned tentatively to *Homo sp.* and *H. erectus*) have double-rooted mandibular premolars, with the exception of ER 992,

TABLE 4.15

Mandibular premolar root morphology in 'early' Homo (after Abbott, 1984)

	Olduvai Gorge			*Homo sp.* / *H. erectus*	
	P_3	P_4		P_3	P_4
OH 7	1R(T)	1R(?T)	ER 730	2R:MB+D	?2R:M+D
OH 13	1R(T)	1R	ER 992	?2T	1R
OH 16	1R(T)	1R	ER 1483	1R(T)	1R(T)
OH 22	1R(?T)	1R	ER 1801	2T	2R:M+D
OH 23	1R(T)	1R(T)	ER 1802	?2R:M+D	?2R:M+D
OH 37	1R(?T)	1R(T)	ER 1805	?2R:MB+D	-
OH 51	2T	2R:M+D	ER 3734	2T	2R:M+D
			BK 8518[1]	-	2R:M+D
			SK 15[2]	?2T	-

Key:

1R	Single root
1R(T)	Single Tomes' root (bifurcation at < 50% of root height)
2T	Double Tomes' root (bifurcation at >= 50% of root height)
2R:MB+D	Double root: mesiobuccal and distal
2R:M+D	Double root: mesial and distal

Note: Data are from Abbott (1984) except:

1. Wood and Van Noten (1986)
2. Robinson (1953: Figure 12)

which has a single-rooted P_4, and ER 1483, which has a single Tomes root in both lower premolars. BK 8518 and SK 15 each have a premolar root morphology which is consistent with either Homo sp. or H. erectus.

In their diagnosis of H. habilis, L.S.B. Leakey et al. (1964) emphasised that the buccolingual narrowing of the lower cheek teeth in this species was accompanied by an elongation of the talonid in the premolars and a rearrangement of the distal cusps in the molars. Wood et al. (1983) analysed mandibular molar relative cusp areas and fissure patterns in different taxonomic groups of Plio-Pleistocene hominids. Using Principal Components Analysis they found that specimens attributed to EAFHOM had relatively large protoconids, and clustered at the opposite pole to the more robust taxa which tended to possess relatively large hypoconulids and entoconids (Wood et al., 1983: Figure 5). Their analysis of the fissure patterns for M_1 essentially confirmed this picture.

Wood et al. (1983) did not investigate the pattern within EAFHOM, but Uytterschaut (personal communication) has provided me with data that allow such an investigation to be undertaken. These data show that the Olduvai gracile hominids form a separate cluster from that of the Koobi Fora gracile hominids. For M_1, the enlarged protoconid is essentially confined to the Koobi Fora hominids, although OH 13 also possesses a relatively large protoconid. OH 7 and OH 16 are close to the SAFROB/SAFGRA distribution in which the distal cusps of M_1 are enlarged. M_1 fissure pattern (Wood et al., 1983: Figure 8) confirms this pattern of relationships. OH 13 and OH 16 are closer to the SAFROB/SAFGRA hominids than they are to the Koobi Fora EAFHOM distribution. Principal components analyses of relative cusp areas in P_3 and P_4 also distinguish Olduvai hominids (OH 6, OH 7, OH 13, OH 16 and OH 22) from Koobi Fora specimens including ER 992 and ER 1802 (Uytterschaut, personal communication).

Data for enamel thickness and structure in East African hominids are provided by Beynon and Wood (1986). Their data support a distinction between EAFHOM and EAFROB, but do not appear to substantiate any distinction between Olduvai and Koobi Fora samples of EAFHOM.

CHAPTER 5: PHYLOGENETIC ANALYSIS OF FOSSIL HOMINIDS

5.1 Details of phylogenetic methods

5.2 Results of phylogenetic analysis

5.3 Discussion

CHAPTER 5: PHYLOGENETIC ANALYSIS OF FOSSIL HOMINIDS

5.1 Details of phylogenetic methods

5.1.1 Approach

Preamble

As noted in 1.2.5 above, there are several reasons why methods of phylogenetic reconstruction that rely on observation of gross morphology, though applicable to other animal groups, might fail to resolve relationships among hominids. The principal reasons given earlier were (A) that hominids, *qua* primates, are generalised mammals that lack highly diagnostic characters; (B) that neoteny confounds reconstructions of their character evolution; and (C) that hominids adapt culturally rather than somatically.

The first of these reasons may be less significant than it initially appears. At least some hominids share specialisations (such as bipedalism) that are unique among primates, while many of the derived characters that distinguish *Homo sapiens* from other primates are evident to a greater or lesser extent in skeletal morphology. It is probable that some of the characters that are derived in *Homo sapiens* also serve to delineate taxonomic subgroups of the Hominidae. Thus there are reasonable prospects that hominid phylogeny might be resolved using morphological criteria.

Some features of the adult human appear neotenous by comparison with extant primates (Gould, 1977). There are, however (as Gould acknowledges) regions of the skeleton in which human development is accelerated so that the adult form is peramorphic by comparison with other primates. Even within anatomical regions that are characteristically neotenous in humans, certain features may be strongly recapitulatory (e.g. mastoid development compared to other structures in the cranial base; although Dean and Wood (1984) argue that the human cranial base is not 'essentially neotenous', their argument is founded on a baseline for comparison - birth - that is strongly heterochronic between humans and other primates). Neoteny can be regarded as a potential source of homoplasy that is best countered by a rigorous character sampling strategy such as that adopted in the present study. Furthermore, recent studies of hominid maturation rates suggest that if human neoteny is attributable to ontogenetic retardation (as Gould (1977) has claimed) then its effects may be largely confined to the more recent stages of human evolution.

Hominid cultural innovation, if judged by its putative effects (e.g. the ability to exploit a wider range of food resources), must be ranked alongside morphological adaptation as an important factor in human evolutionary biology. It is arguable, however, whether culture need either deter speciation (as proposed by Mayr (1950) and Robinson (1954)), or serve as a substitute for morphological change. Indeed, culture and morphology may coevolve. Plausible explanations for human ontogenetic retardation and its consequence, neonatal dependence, evoke social and cultural factors such as food sharing and use of a home base. As a further example, reduction in the gnathic apparatus in human evolution may be related to an increasing incidence of extraoral food preparation. There is no evidence that culture deters speciation. The first securely-dated appearance of stone tools at around 2 Myr (Isaac, 1984) is preceeded by speciation in Australopithecus and postdated by speciation in Homo. Thus there would seem to be no overiding reasons why morphological information should not be used as a basis for estimating phylogenetic relationships among hominids.

Strategy

Arnold (1981) has offered useful guidelines for cladistic analysis at low taxonomic levels. Arnold identified a series of methodological problems that particularly affect studies of closely related organisms. His recommendations for countering these difficulties include sampling a large number of characters distributed across a range of organs and systems; inclusion of all known taxa of a group; use of more than one method of polarity determination; and the sampling of all intraspecific variation (sexual, ontogenetic, geographic etc.).

In the present study of Pliocene to Recent hominids a large number of characters have been sampled in order to undertake metrical comparisons between individuals and groups. There seemed to be no reason why these same characters should not be employed for cladistic analysis, provided some means of inferring their polarity was available. Ontogenetic information is perhaps the most reliable indicator of character polarity (Nelson, 1978; Bonde, 1984), but is not readily obtainable for the characters used in this study. Juvenile specimens tend to be poorly preserved in the hominid fossil record, and are apparently less easily attributable to species.

Outgroup analysis is the method adopted here to determine character polarity. Maddison _et al._ (1984) discuss various approaches to outgroup analysis and recommend that when relationships among several outgroup taxa are already well resolved this knowledge should be used to synthesise a hypothetical ancestral taxon that represents the 'outgroup node' (most recent common ancestor of the ingroup and its closest outgroup). They recommend that the hypothetical ancestral taxon then be included with the ingroup terminal taxa in a maximum parsimony analysis in order to find the most parsimonious 'global' solution for ingroup and hypothetical outgroup taxon combined. Maddison _et al._ (1984) implicitly assume that the same morphological characters are to be used to determine both ingroup and outgroup relationships.

There are, however, no _a priori_ reasons why different characters should not be recruited in order to establish the pattern of outgroup relationships. In the present study the outgroup taxa are extant primate species whose phylogeny has been investigated by other workers using the techniques of molecular biology. According to Andrews (1986), who has reviewed the molecular evidence, the catarrhine primates comprise two monophyletic superfamilies, the Cercopithecoidea and the Hominoidea. The phylogeny of the non-human hominoid species is determined by a variety of molecular evidence - only the branching point of the

Hominidae is subject to uncertainty (Andrews, 1986). Thus the preliminary outgroup analysis recommended by Maddison et al. (1984) reduces to the straightforward task of tracing the evolution of morphological characters on the molecular cladogram for the outgroup taxa. The 'consensus' molecular cladogram for the outgroup taxa is given in Figure 5.01.

In the preceding comparative study, the characters were quantified as linear measurements and then transformed into dimensionless shape attributes using Kazmierczak's transformation. These 'shape' variables were then coded as discrete character states so that Mean Character Difference could be used as a measure of taxonomic distance between individuals or group centroids. The same character states provide the raw data for the phylogenetic analyses that follow. Currently available microcomputer phylogeny programs require character states to be defined as discrete rather than continuous values (Fink, 1986), and the loss of information that results from coding continuous variables as discrete character states is offset by the faster computations achieved with discrete data.

The program used in this study was PAUP (Swofford, 1985) which has options for treating characters as ordered or non-ordered, and which also has the facility to weight characters inversely according to the number of character states into which each character has been divided. The characters used in this study were by definition ordered, because they were based on transformed linear measurements: the states of each character are a series of integers that represent a morphocline extending from a structure that is relatively small to

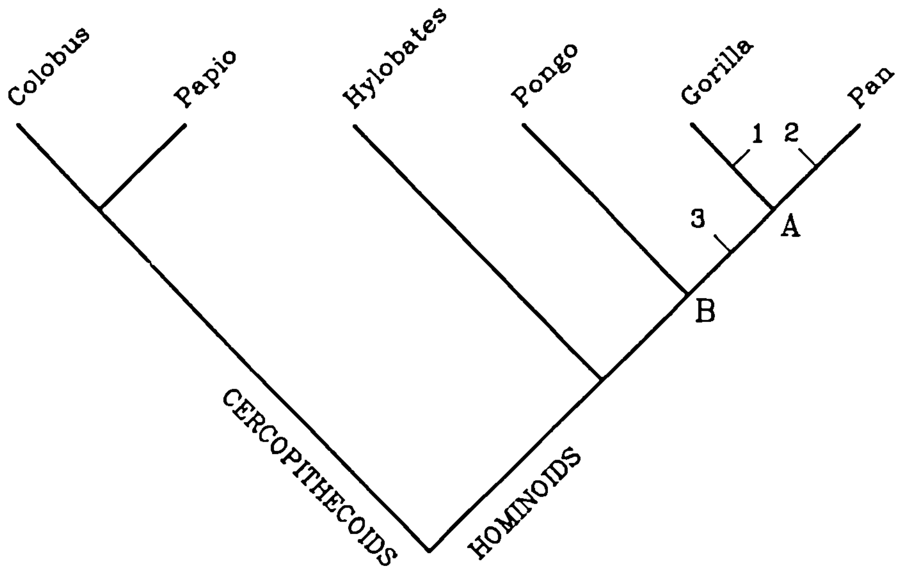


Figure 5.01

Consensus molecular cladogram for the outgroup taxa

Character states at Node A are a conservative estimate of the hypothetical common ancestor of hominids if the latter are most closely related to Gorilla (1) or Pan (2). The character states at Node B provide a better estimate of the common ancestor if the hominids are the sister group (3) of an African ape clade.

one which is relatively large compared to the 'average' primate. There is a strong case for inversely weighting characters according to the number of states of each character, provided that the number of character states has been determined arbitrarily. My view, however, is that such weighting is unwarranted in this instance. For all characters used in this study the difference between adjacent character states represents proportionally the same amount of shape difference. Thus characters that exhibit fewer character states can be regarded as being evolutionarily conservative. Nonetheless, the effect on a cladogram of weighting according to the number of character states was investigated.

5.1.2 Reconstruction of a hypothetical hominid ancestor

The procedure used for reconstructing the morphotype of a common ancestor is referred to as 'optimisation' (Swofford, 1985). Given a set of terminal taxa and their character states, the cladogram for those taxa not only depicts the pattern of relationship among those taxa but also (in conjunction with the principle of parsimony) implies a pattern of character evolution. For every character that is fully consistent on the cladogram (i.e. exhibits no homoplasy) there is only one possible character state assignment at each internal node of the cladogram, if the cladogram is to be of minimal length (Swofford, 1985). However, if a character exhibits homoplasy (i.e. there is either a reversal, or two independent appearances of a derived character state) then there are often several possible assignments of different character states at a given internal node, each assignment yielding a cladogram of the same length. The PAUP phylogeny program is able to determine all equally-parsimonious interpretations of the internal nodes of a cladogram, and the program also provides optimisation procedures that deal in different ways with this ambiguity over character evolution.

One of the optimisation procedures in PAUP is called 'MINF', and it has the effect of transferring evolutionary steps from interior branches of the cladogram towards terminal branches wherever possible. This option thereby minimises the possibility that internal nodes of the cladogram will be defined by an arbitrary choice of derived character state. MINF optimisation was used in the reconstruction of the ancestral morphotype so that where there was any uncertainty in character state assignment the morphotype was reconstructed as being more like a generalised hominoid (i.e. more like the common ancestor of gibbons and great apes) and less like a large-bodied great ape.

The 'consensus' molecular cladogram for the outgroup taxa is depicted in Figure 5.01. Molecular comparisons indicate that modern Homo sapiens has closest affinities with Pan and Gorilla, but the trichotomy between these three taxa is unresolved (Groves, 1986; Savatier et al., 1987). Since I have defined hominids as those taxa whose recent common ancestor is most closely related to Homo sapiens among living species, and H. sapiens in turn is most closely related to Pan and Gorilla, hominids as a group must be linked to the outgroup cladogram at one of three possible positions (labelled 1, 2 and 3 in Figure 5.01). If the branching point for hominids was either 1 or 2 in Figure 5.01 then one could select Node A as providing a suitable estimate for the hominid common ancestor. If, however, the branching point for hominids was at position 3 then character states at Node A might be derived in a direction away from that branching point, and instead represent synapomorphies of an African ape clade. Therefore the character states at the previous node (labelled B on Figure 5.01) were chosen because they provide a conservative estimate of the hypothetical hominid ancestor.

For each character the raw measurements of the pooled sex samples of 20 crania and mandibles were averaged within each of the six non-human primate taxa. The averaged measurements were then converted into sets of character states for each taxon, using the procedure described in section 3.3.3 above. The resulting character state matrix for the outgroup taxa (Table 5.01) was optimised to the topology of the outgroup cladogram using the PAUP program. The optimised character states at Node B were obtained using the MINF option, and they are listed in Table 5.01.

5.1.3 Sample of fossil hominids

The hominid taxa included in the phylogenetic analysis were modern _H. sapiens_ and all of the fossil taxa listed in Table 4.04. 'Early' _Homo_ was thus subdivided into _H. habilis_ (sensu stricto) and _Homo sp._ The hypodigms of the fossil taxa were as listed in Table 4.04, except with the addition of mandibles ER 730 and 992 to 'African' _H. erectus_ and the addition of ER 1802 to _Homo sp._ These additional attributions are not incompatible with the comparative evidence presented in

TABLE 5.01

Character state matrix for the outgroup taxa and hominid common ancestor

CHARACTERS	B01	B02	B03	B04	B05	B06	B07	B08	B09	B10	B11	B12	B13	B14	B15	B16	V01	V02	V03	V04	V05	V06	V07	V08	V09	V10	V11	V12	V13	F01
Colobus	4	4	4	5	4	4	4	4	5	4	3	4	5	5	4	5	1	4	4	4	4	4	4	4	2	4	2	4	2	4
Papio	4	3	2	4	4	3	4	4	4	3	3	3	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	3
Hylobates	5	4	5	4	5	3	5	5	5	5	5	5	5	4	5	5	0	5	5	5	5	6	3	6	4	6	4	5	5	5
Pongo	4	4	4	3	4	5	4	4	4	4	4	4	4	4	4	4	5	3	4	4	3	3	3	4	4	3	3	4	3	3
Gorilla	4	4	4	4	3	5	4	4	4	4	4	4	4	4	4	4	3	3	3	4	4	3	3	3	4	3	4	3	3	4
Pan	4	4	4	4	4	4	5	4	4	4	4	4	4	4	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4
Ancestor	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	4	4	4	3	3	4	4	3	3	4	3	4

CHARACTERS	F02	F03	F04	F05	F06	F07	F08	F09	F10	F11	F12	F13	F14	F15	F16	F17	F18	F19	M01	M02	M03	M04	M05	M06	M07	M08	M09	M10	M11	M12
Colobus	4	4	4	4	4	5	4	3	3	3	2	3	3	5	4	4	7	5	4	5	5	5	4	5	4	3	4	4	5	5
Papio	4	4	4	3	4	2	4	4	6	6	6	4	4	4	5	4	5	7	5	5	4	5	3	5	4	3	3	5	5	5
Hylobates	4	4	4	5	5	6	6	4	2	3	2	4	2	5	4	4	4	5	3	3	3	2	2	2	3	4	5	4	4	4
Pongo	4	4	3	3	3	2	1	3	4	4	4	4	4	3	4	4	0	3	5	5	5	4	5	4	5	5	4	5	5	4
Gorilla	4	4	4	4	4	4	6	4	4	4	5	5	5	4	4	4	3	5	4	4	4	4	5	5	4	4	3	4	4	4
Pan	4	4	5	4	4	5	3	4	4	4	4	4	4	4	4	4	3	3	4	4	4	2	4	4	4	5	4	5	3	3
Ancestor	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	5	4	5	4	4	4	4	4	4	4	5	5	4

CHARACTERS	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	P01	P02	P03	P04	P05	P06	P07	P08	P09	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20
Colobus	4	4	5	4	5	5	4	4	5	4	4	4	4	4	4	3	3	4	5	5	3	3	4	4	4	4	4	4	5	4
Papio	5	5	4	4	6	3	4	4	6	5	5	4	4	4	5	3	6	5	4	5	5	5	4	4	4	3	5	4	5	5
Hylobates	3	3	4	4	4	3	4	4	3	3	4	4	4	5	1	4	4	4	4	4	3	3	4	5	5	4	4	4	3	4
Pongo	5	5	4	4	4	5	4	4	4	4	4	4	5	4	6	4	5	5	4	4	5	5	5	4	5	5	4	4	4	4
Gorilla	4	3	4	4	4	5	4	4	4	4	4	4	4	3	4	4	4	4	4	4	4	4	5	4	4	5	4	4	4	4
Pan	5	5	5	5	3	4	4	4	3	4	4	4	5	4	3	4	4	5	4	4	5	4	4	4	4	4	4	4	3	4
Ancestor	5	5	4	4	4	5	4	4	4	4	4	4	4	4	4	4	4	5	4	4	5	4	4	4	4	4	4	4	4	4

Note: 'Ancestor' is the morphotype of Node B on Figure 5.01, optimised using the MINF option in PAUP. Abbreviated definitions of characters are given in Table 4.14, and full definitions are given in Appendix 2. Character states range from 0 (relatively small) to 8 (relatively large).

Chapter 4 and the stratigraphic evidence discussed in Chapter 6. The similarity of mandibles tentatively attributed to *Homo sp.* and 'African' *H. erectus* implies that even if these mandibles prove to be incorrectly assigned they are unlikely to seriously affect the outcome of any phylogenetic analysis involving these taxa. An earlier analysis (Chamberlain and Wood, in press) showed that the affinities of *Homo sp.* are not affected by the inclusion of ER 1802 in the hypodigm.

The discontinuous character states for the fossil hominid taxa were computed after averaging the continuous size-standardised characters within each taxon. The character state matrix for the fossil hominids and the ancestral (outgroup) taxon is given in Table 5.02.

TABLE 5.02

Character state matrix for the ingroup taxa and the hominid ancestor

CHARACTERS	B01	B02	B03	B04	B05	B06	B07	B08	B09	B10	B11	B12	B13	B14	B15	B16	V01	V02	V03	V04	V05	V06	V07	V08	V09	V10	V11	V12	V13	F01
Ancestor	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	4	4	4	3	3	4	4	3	3	4	3	4
A. afarensis	4	5	7	5	-	5	3	4	4	-	-	5	-	-	-	-	6	-	4	5	-	-	-	-	4	-	4	-	-	-
A. africanus	3	4	4	4	4	4	2	4	4	4	4	4	4	3	4	3	6	3	4	4	4	4	5	4	4	4	4	4	4	3
A. robustus	-	-	-	-	-	5	4	-	4	4	-	-	5	-	-	-	6	4	-	4	-	3	-	-	-	3	-	-	-	4
A. boisei	4	5	3	5	4	5	4	4	4	4	3	4	6	5	4	3	6	3	3	4	4	3	5	2	3	3	3	3	3	4
Homo sp.	4	4	3	3	4	4	4	4	4	5	-	-	5	3	4	-	7	4	4	4	4	4	5	4	5	4	5	5	5	4
H. habilis	4	4	4	4	4	3	3	3	3	4	4	4	-	-	-	-	5	4	-	4	-	-	4	-	4	-	4	-	5	-
Afr. erectus	4	4	4	4	4	4	3	4	3	4	4	4	3	3	3	3	7	4	5	4	5	4	4	4	5	4	6	4	5	4
Asi. erectus	3	3	4	3	-	4	3	3	4	-	5	4	-	-	-	2	8	-	5	4	-	-	5	4	5	-	5	4	6	-
Arc. sapiens	3	5	4	4	4	3	2	3	2	3	4	4	2	3	3	3	8	5	5	4	5	5	5	5	5	5	6	5	6	4
Mod. sapiens	4	5	5	5	5	3	2	3	3	3	5	5	3	3	4	3	7	5	5	4	6	6	7	6	7	6	7	6	7	4

CHARACTERS	F02	F03	F04	F05	F06	F07	F08	F09	F10	F11	F12	F13	F14	F15	F16	F17	F18	F19	M01	M02	M03	M04	M05	M06	M07	M08	M09	M10	M11	M12
Ancestor	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	5	4	5	4	4	4	4	4	4	4	5	5	4
A. afarensis	4	-	4	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	3	4	4	4	4	4	6	4	4	3	3	4
A. africanus	4	5	4	4	4	4	2	5	3	4	4	4	6	4	4	4	4	1	3	4	4	5	5	4	6	3	5	3	3	4
A. robustus	-	4	4	5	4	6	-	5	-	3	4	4	6	4	4	5	5	0	4	4	4	4	6	5	6	3	-	2	3	5
A. boisei	5	4	4	4	4	5	3	4	4	5	5	5	6	4	4	6	4	0	3	4	4	6	6	5	7	3	4	2	4	5
Homo sp.	4	4	4	4	4	5	2	4	4	3	4	4	4	4	3	4	4	0	3	4	4	5	5	5	6	3	4	2	3	4
H. habilis	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	4	5	5	4	6	4	4	3	4	4
Afr. erectus	4	4	4	4	4	4	3	4	3	-	4	4	5	4	3	3	3	0	3	4	4	5	5	5	6	4	4	3	3	4
Asi. erectus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	4	4	4	5	3	5	4	-	4	3	4
Arc. sapiens	4	4	5	4	4	6	4	5	3	4	4	4	4	4	3	3	6	2	3	4	4	4	4	4	6	5	6	3	3	4
Mod. sapiens	4	4	5	4	4	5	4	4	3	3	3	3	3	4	3	4	6	1	3	4	4	6	5	4	5	4	6	3	3	4

CHARACTERS	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	P01	P02	P03	P04	P05	P06	P07	P08	P09	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20
Ancestor	5	5	4	4	4	5	4	4	4	4	4	4	4	4	4	4	4	5	4	4	5	4	4	4	4	4	4	4	4	4
A. afarensis	4	4	3	3	3	5	4	5	5	5	3	4	4	3	2	3	2	2	4	5	4	3	2	3	4	4	4	4	5	5
A. africanus	3	3	3	3	3	5	5	5	4	5	4	5	4	4	5	6	0	3	4	5	-	-	-	-	4	5	4	5	6	5
A. robustus	3	2	2	2	3	5	5	5	4	5	4	5	3	4	3	4	0	3	5	5	-	-	1	3	4	5	4	5	5	5
A. boisei	2	2	1	2	3	5	4	5	5	5	3	5	3	3	5	5	0	2	5	5	3	3	1	3	5	6	4	6	5	6
Homo sp.	-	-	-	-	3	5	5	5	5	4	3	5	3	4	5	4	0	3	4	5	3	2	2	3	4	4	5	5	5	5
H. habilis	4	3	3	3	3	4	5	5	5	5	3	4	4	4	-	4	-	-	4	4	-	-	-	-	4	4	4	4	4	4
Afr. erectus	-	-	4	2	3	5	4	4	4	4	-	4	4	3	7	5	3	-	2	-	-	-	-	-	4	4	4	4	-	-
Asi. erectus	-	-	3	3	3	5	5	5	4	4	3	5	4	4	6	5	3	4	4	4	-	-	2	3	4	4	4	4	3	4
Arc. sapiens	3	4	3	3	2	4	5	5	4	4	2	4	3	5	4	4	0	3	3	3	-	3	2	3	3	3	3	4	2	3
Mod. sapiens	3	3	3	3	2	4	5	5	4	5	2	4	3	5	4	4	0	3	3	3	3	3	1	3	3	3	4	4	3	4

5.2 Results of phylogenetic analysis

5.2.1 Overall cladogram

The maximum parsimony tree for the hominid character state matrix was obtained using the PAUP program. The branch and bound algorithm was employed to ensure that the shortest tree was obtained. The resulting tree was rooted to form a cladogram (Figure 5.02) by placing the outgroup taxon as the sister group of all other taxa. This most parsimonious cladogram indicates that the affinities of *Homo sp.* lie with the 'robust' australopithecines (a similar relationship, though phenetic rather than cladistic, was noted in 4.1.2 above). In other respects the cladogram of Figure 5.02 is consistent with the phylogenetic hypothesis advocated by Kimbel *et al.* (1984); *A. afarensis* is placed as the sister group of all other hominids, while *A. africanus* is cladistically related to the 'robust' australopithecines (see Figure 2.07 above for Kimbel *et al.*'s cladogram). Figure 5.02 also shows that the detailed relationships of *Homo* (excluding *Homo sp.*) are resolved, with *H. habilis* placed as the sister taxon of a clade comprised of *H. erectus* and *H. sapiens*.

The stability of the most parsimonious cladogram was investigated by seeing whether different arrangements of taxa emerged under character weighting, or after the elimination of individual taxa, and by examining the effect of changes in topology on the overall length of the tree.

Character weighting

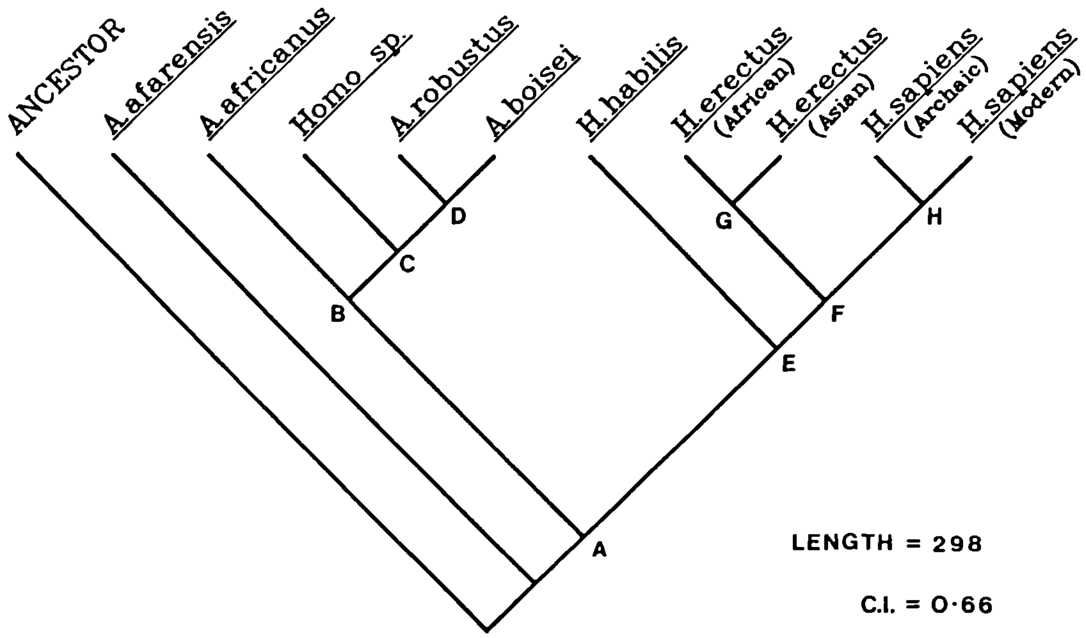


Figure 5.02 Most parsimonious cladogram for hominid taxa

The possible undue influence of characters with a large number of character states was tested by recalculating the maximum parsimony tree after weighting characters inversely according to their number of states. The most parsimonious cladogram using these weighted characters only differed from that of Figure 5.02 by marginally favouring the placement of *H. habilis* as the sister taxon of the *H. sapiens* clade; the position of the other taxa remained unchanged. The inverse weighting procedure probably reduces the influence of characters of the cranial vault, which exhibit a wide range of character states among hominids (Table 5.02) and are particularly instrumental in linking *H. erectus* with *H. sapiens*.

Deletion of taxa

The most parsimonious cladogram was also recalculated after *H. habilis* had been removed from the character state matrix. There were several equally parsimonious arrangements of the remaining taxa. In one of these cladograms *Homo sp.* was placed as the sister taxon of later species of *Homo* (*H. erectus* and *H. sapiens*). In the other equally parsimonious cladograms *Homo sp.* retained its position as the sister group of the 'robust' australopithecines, but there were alternative arrangements among the later species of *Homo*.

When *Homo sp.* was removed from the character state matrix, two equally parsimonious arrangements of the remaining taxa were found. In one of these cladograms the relationships among the remaining taxa were identical to those in Figure 5.02 (i.e. the removal of *Homo sp.*

made no difference). In the other cladogram A. africanus was placed as the sister group of the Homo clade, with the positions of the other taxa being unchanged.

Deletion of the 'robust' australopithecines allowed several equally parsimonious best-fit cladograms to be constructed. These cladograms most commonly placed Homo sp. and A. africanus as sister taxa, and linked H. habilis either with the H. sapiens clade or as the sister taxon of all hominids apart from A. afarensis.

Some inferences can be made from the response of the most parsimonious cladogram to the removal of subclades from it. When H. habilis is removed from the analysis, Homo sp. shows some affinities with H. erectus and H. sapiens. When Homo sp. is removed A. africanus also shows some affinities with Homo. However, both A. africanus and Homo sp. continue to be linked cladistically with the 'robust' australopithecines in most of the cladograms despite removal of single taxa.

Modification of cladogram topology

Another method for investigating the strength of relationships depicted on a cladogram is to calculate the increase in homoplasy that is implied by alternative arrangements of the ingroup taxa. The 'user-tree' option in the PAUP phylogeny program allows the calculation of the length (number of character state changes) and Consistency Index (a measure of homoplasy) of a tree of a given topology.

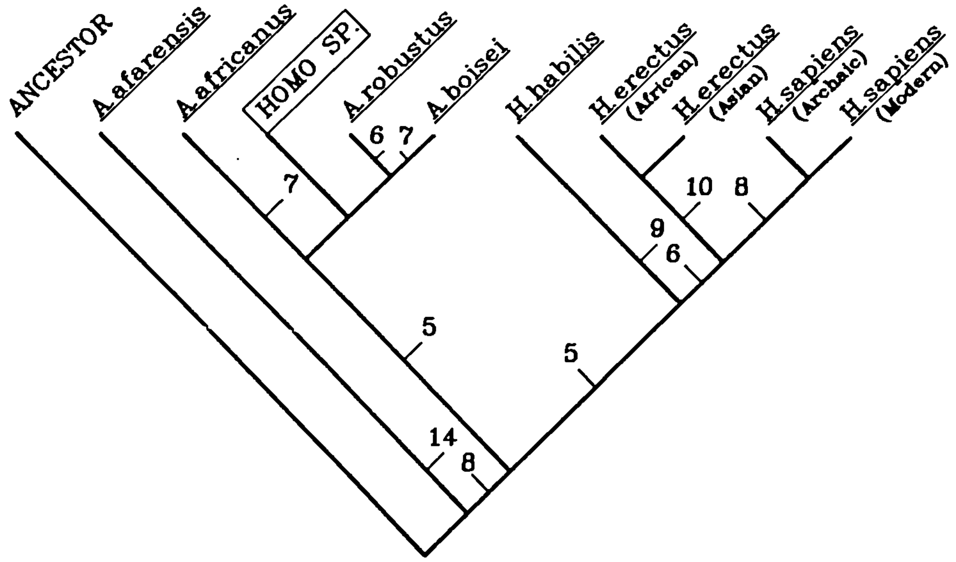


Figure 5.03 Number of extra evolutionary steps (character state changes) required if Homo sp. were to be repositioned on the most parsimonious cladogram.

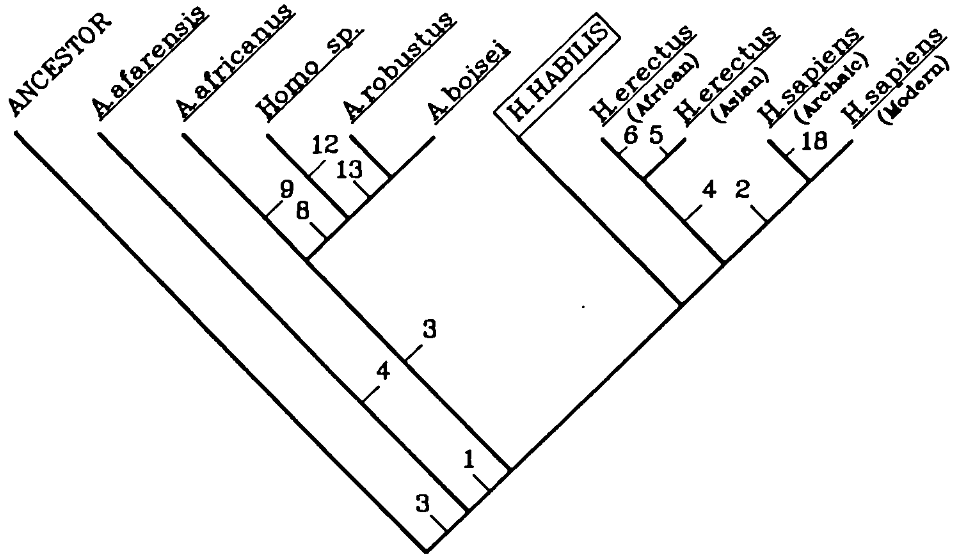


Figure 5.04 Number of extra evolutionary steps (character state changes) required if H. habilis were to be repositioned on the most parsimonious cladogram.

Figure 5.03 illustrates the number of extra evolutionary steps (character state changes) that would be required if Homo sp. were to be removed from its position as the sister group of the 'robust' australopithecines and replaced at various other points on the tree. The data indicate that a minimum of five extra evolutionary steps would be incurred for any repositioning of Homo sp. that left the positions of other taxa unchanged.

In Figure 5.04 the number of extra steps incurred by repositioning H. habilis is indicated. These data show that relatively little extra homoplasy is required when H. habilis is placed either more distally (towards the base of the cladogram) or as the sister taxon of H. erectus or H. sapiens. There is a considerable increase in the number of evolutionary steps, however, if H. habilis is placed as a member of the A. africanus/Homo sp./'robust' australopithecine clade. It should be noted that to some extent the low cost of moving H. habilis may be attributable to the fact that this species has a larger proportion of missing data than does Homo sp. (see the character state matrix, Table 5.02).

The extra cost of repositioning A. africanus is shown in Figure 5.05. A. africanus can be placed either as the sister group of Homo, or as the sister group of a clade of all hominids other than A. afarensis, with little additional homoplasy. Other arrangements of A. africanus imply substantially greater increases in homoplasy. Unlike H. habilis, A. africanus has very few missing data values. Thus the fact that A. africanus can be repositioned on the cladogram with

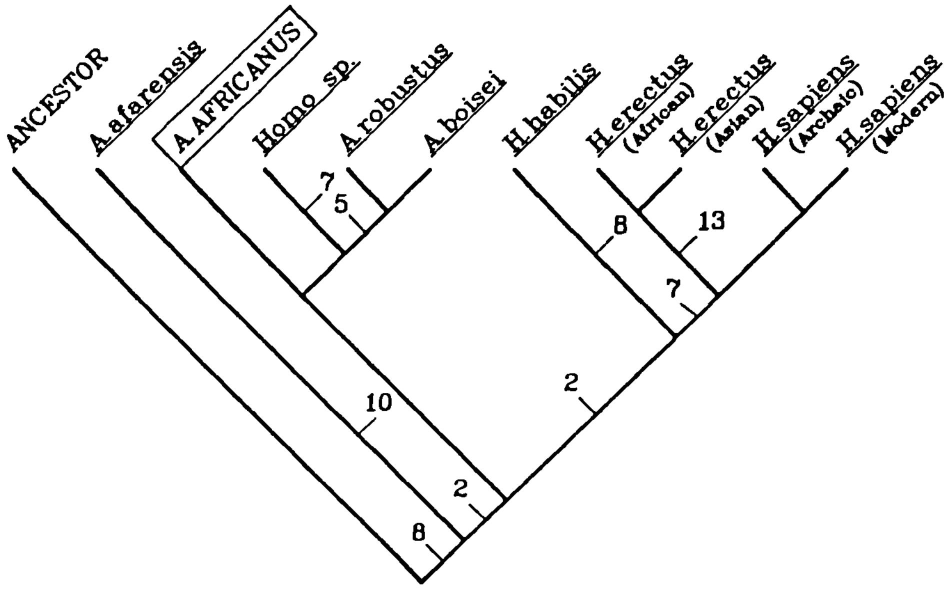


Figure 5.05 Number of extra evolutionary steps (character state changes) required if A.africanus were to be repositioned on the most parsimonious cladogram.

little change in overall tree length indicates that this species' affinities with some other taxa are equivocal.

Overall, the results of these manipulations of the topology of the maximum parsimony cladogram indicate that the branching order of four clades has not yet been fully established. These clades are A. africanus, H. habilis, Homo sp./A. robustus/A. boisei, and H. erectus/H. sapiens. Within the latter two clades the relationships among the species are moderately well defined. H. habilis appears to be a primitive hominid that nonetheless has some affinities with H. erectus and H. sapiens. A. africanus, which appears to be little differentiated from the shared morphotype of all hominids that postdate the divergence of A. afarensis, nonetheless exhibits slight affinities with the Homo sp./'robust' australopithecine clade.

Effect of including the hypothetical ancestor in the analysis

The inclusion of the hypothetical ancestor in the analysis might have had some effect on the internal arrangement of sister-group relationships among the ingroup taxa. This possibility was investigated by deleting the hypothetical ancestor from the character state matrix and then finding the most parsimonious tree for the ingroup taxa alone. This tree was then rooted by placing A. afarensis as the sister group of all other hominids (in effect, this is to assume that A. afarensis is the most primitive hominid). The resulting most parsimonious arrangement was identical to that of Figure 5.02, indicating that inclusion of the ancestor (for the purpose of establishing a root) does not influence the pattern of ingroup relationships.

5.2.2 Shared derived characters

The character states defining the internal nodes of the most parsimonious ingroup cladogram were determined (as for the outgroup cladogram) by MINF optimisation. The internal nodes are labelled A to H on Figure 5.02. The character state changes at a particular node are the differences between the character states at that node and those at the immediately preceding node (direction is from the base of the cladogram upwards). Thus the character state changes are the synapomorphies that define the monophyletic group of taxa whose common ancestor is represented by the node. These character state changes can be interpreted biologically by referring to the character definitions (Table 4.14 and Appendix 2) Since all specimens were standardised for size, when the terms 'increase' and 'reduction' are used here they refer to relative, and not absolute sizes of anatomical structures.

The large number of character state changes at the basal node of the ingroup cladogram (the 'ingroup node') are not listed because they are an artefact of the choice of outgroup, which in this instance was estimated conservatively (i.e. the outgroup was more 'primitive' than it perhaps needed to be). Character state changes at nodes A to H are listed in Table 5.03.

Nodes A and B are defined solely by characters of the mandible and

TABLE 5.03

Shared derived characters defining nodes of the ingroup cladogram

Key:		
	M1	Increase in character M1 by one character state
	$M1^2$	Increase in character M1 by two character states
	$\underline{M1}$	Decrease in character M1 by one character state
	$\underline{M1}^2$	Decrease in character M1 by two character states

Node A: All hominids except A. afarensis

M4	Increased height of foramen spinosum
M5	Increased height of mental foramen
$\underline{M13}$	Reduced M-D diameter of I_1
$\underline{M14}$	Reduced B-L diameter of I_1
P5	Increased anterior palate depth
$\underline{P7}^2$	Reduced anterior palate projection
$\underline{P11}$	Reduced M-D diameter of I^1

Node B: A. africanus, Homo sp. and 'robust' australopithecines

$\underline{M8}$	Reduced breadth between lower canines
P2	Increased external palate breadth
P10	Increased length of upper molar alveolar row
P18	Increased B-L diameter of M^1
P19	Increased M-D diameter of M^3
P20	Increased B-L diameter of M^3

Node C: Homo sp. and 'robust' australopithecines

$\underline{B3}$	Reduced breadth between petrous apices
B7	Increased length of tympanic plate
B13	Increased length of temporal fossa
F7	Increased interorbital breadth
$\underline{F19}$	Reduced maxillary prognathism
M6	Increased depth of mandibular symphysis
$\underline{M10}$	Reduced length of lower incisor alveolar row
$\underline{P3}$	Reduced breadth between upper canines

Node D: 'Robust' australopithecines

B6	Increased mediolateral breadth of mandibular fossa
$\underline{V6}$	Reduced frontal sagittal chord
$\underline{V10}$	Reduced frontal sagittal arc
$F14^2$	Increased height of zygomaxillare
F17	Increased zygomaxillary prognathism
M5	Increased height of mental foramen
M12	Increased length of lower molar alveolar row
$\underline{M15}$	Reduced M-D diameter of C_1
$\underline{M16}$	Reduced B-L diameter of C_1
P9	Increased length of upper premolar alveolar row
$\underline{P13}$	Reduced M-D diameter of C^1
P16	Increased B-L diameter of P^3

TABLE 5.03 [Contd.]

Node E: H. habilis, H. erectus and H. sapiens

B8	Reduced length of petrous temporal
B9	Reduced distance from foramen ovale to carotid canal
V13	Increased posterior cranial length

Node F: H. erectus and H. sapiens

B13	Reduced length of temporal fossa
V1	Increased thickness of cranial vault
V3	Increased biporionic breadth
V5	Increased length of cranial vault
V9	Increased occipital sagittal chord
V11	Increased occipital sagittal arc
F16	Reduced alveolar prognathism
P19	Reduced M-D diameter of M^3

Node G: Asian and African H. erectus

M22	Reduced B-L diameter of M_3
P5	Increased anterior palate depth
P6	Increased posterior palate depth
P7^2	Increased anterior palatal projection

Node H: 'Archaic' and 'modern' H. sapiens

B2	Increased breadth between carotid canals
B6	Reduced mediolateral breadth of mandibular fossa
B7	Reduced length of tympanic plate
B10	Reduced distance from infratemporal crest to carotid canal
V2	Increased postorbital breadth
V6	Increased frontal sagittal chord
V8	Increased parietal coronal chord
V10	Increased frontal sagittal arc
V11	Increased occipital sagittal arc
V12	Increased height of vertex
V13	Increased posterior cranial length
F4	Increased breadth between infraorbital foramina
F7	Increased interorbital breadth
F8	Increased breadth of piriform aperture
F18^2	Increased projection of nasion
M9^2	Increased breadth between lower molars
M17	Reduced M-D diameter of P_3
M18	Reduced B-L diameter of P_3
P1	Reduced palate length
P3	Reduced breadth between upper canines
P4	Increased breadth between upper molars
P5	Reduced anterior palate depth
P9	Reduced length of upper premolar alveolar row
P10	Reduced length of upper molar alveolar row
P15	Reduced M-D diameter of P^3
P16	Reduced B-L diameter of P^3

palate. Node A (the sister group of *A. afarensis*) is defined by a deepening of the inferior part of the mandibular corpus, by a deepening and shortening of the anterior palate, and by a reduction in the size of the incisors. These are classic 'hominid characters', and serve very well to distinguish, for example, between *Homo sapiens* and *Pan troglodytes*. Node B is defined by several characters that express enlargement of the upper molars, together with a narrowing of the anterior mandibular dental arch. These are more typically 'australopithecine' characters.

The characters at Node C link *Homo sp.* with the 'robust' australopithecines. These characters are distributed across the base, face, palate and mandible. They are heterogeneous, but include some traditional 'australopithecine' characters: reduction in maxillary prognathism, increase in the depth of the mandibular symphysis and further narrowing of the anterior dental arches.

Characters at Node D define the 'robust' australopithecine clade. These characters, for the most part, reflect an enlargement of the masticatory apparatus and of the cheek tooth crowns. Additional characters that distinguish this node include canine reduction and reduced sagittal dimensions of the frontal bone.

Three characters at Node E group *H. habilis* with the later species of *Homo* (*H. erectus* and *H. sapiens*). Two of these characters probably reflect shortening of the anterior cranial base, while the third reflects a rearward expansion of the cranial vault.

A clade containing *H. erectus* and *H. sapiens* is differentiated at Node F, mainly by characters reflecting expansion and thickening of the cranial vault. In addition, alveolar prognathism, length of the upper molar alveolar row and length of the temporal fossa are reduced in these taxa. Only four characters appear to define *H. erectus* as a clade at Node G: three of these characters reflect the shape of the palate. Andrews (1984) has commented that the African specimens attributed to *H. erectus* share few derived characters with the Asian specimens of this species, and the results of this analysis offer some support for his suggestion.

In contrast to the condition in *H. erectus*, numerous derived characters at Node H are shared by 'archaic' and 'modern' forms of *H. sapiens*. Four of these characters reflect changes in basicranial shape; a further seven document an increase in the dimensions of the neurocranium; four characters reflect expansion of the facial skeleton and eleven characters of the mandible and palate largely relate to a reduction and remodelling of the gnathic apparatus.

5.3 Discussion

5.3.1 Comparison with other studies

Cladograms of the Hominidae have been published by a number of authors, and are reviewed in 2.3.3 above (see also Figures 2.01 to 2.10). The most parsimonious cladogram from the present study (Figure 5.02) is consistent with the cladograms published by Tattersall and Eldredge (1977) and Johanson and White (1979), and it is also consistent with the most parsimonious arrangement of data presented in Kimbel *et al.* (1984), and with Skelton *et al.*'s (1986) data when analysed using maximum parsimony criteria (Wood and Chamberlain, in press).

In several of the earlier cladistic studies the affinities of *A. africanus* were unclear. Such is also the case in the present study: *A. africanus* can be placed in different locations near Node A (ancestor of all post-*A. afarensis* hominids) with little increase in overall tree length (Figure 5.05). A more unusual finding is that the affinities of *H. habilis* (sensu stricto) are also equivocal (Figure 5.04). All previous cladistic studies that have examined the relationships between *H. habilis* (sensu lato), H. erectus and *H. sapiens* have unanimously agreed that the former taxon is the sister group of the latter two species. (Bonde, 1976, 1977; Tattersall and Eldredge, 1977; Johanson and White, 1979; Corruccini and McHenry, 1980; White *et al.*, 1981; Chamberlain and Wood, in press). It is interesting that L.S.B. Leakey (1966) argued that *H. habilis* (sensu stricto) might be ancestral to *H. sapiens* and not to *H. erectus*.

The apparent affinities between Homo sp. and Australopithecus (and in particular the association of Homo sp. with A. robustus and A. boisei) are not wholly without precedent. Individually, the three Koobi Fora crania ER 1470, ER 1805 and ER 1813 have each been attributed to, or compared with, the genus Australopithecus. Walker (1976) and Stringer (1986) drew attention to a number of characters in which ER 1470 more closely resembled members of Australopithecus than it did H. erectus or H. sapiens. R.E.F. Leakey (1976b), Holloway (1976), Day (1986b) and Falk (1986) have compared ER 1813 to Australopithecus africanus. Holloway (1976) and Falk (1986) have attributed ER 1805 to Australopithecus, and both Tobias (1980a) and Dean and Wood (1982) have identified similarities between ER 1805 and A. boisei. These attributions should, however, be balanced by the views of a majority of workers who regard the Koobi Fora 'gracile' crania as belonging to Homo rather than Australopithecus (although I know of no author who has placed all three specimens in the same species, as has been advocated here). The apparently 'primitive' nature of H. habilis has been anticipated by the identification of primitive characters in the postcrania of this species, and may receive further support from an examination of the morphology of a recently-discovered partial skeleton from Bed I, Olduvai Gorge (Johanson et al., 1987).

5.3.2 Implications

Several strands of evidence suggest that the pattern of relationships determined in this phylogenetic analysis are neither random nor an artefact of the methods employed. Firstly, the characters that support the most parsimonious arrangement are readily interpretable. The derived characters that determine the internal nodes of the cladogram, when expressed in the terms of the original measurement definitions (Table 5.03), appear to reflect some of the qualitative morphological distinctions that other workers have made among hominid lineages. Secondly, the topology of the maximum parsimony cladogram is consistent with some of the cladograms presented by other authors working with independent data sets. An important test of synapomorphy (and, by extension, of any phylogenetic hypothesis founded on synapomorphy) is agreement with other, independent evidence. Thirdly, the 'australopithecine' nature of *Homo sp.*, and the 'primitive' properties of *H. habilis* are in agreement with some earlier comments made about these groups of hominids. L.S.B. Leakey *et al.* (1964) were criticised for basing their generic attribution of *H. habilis* on the few derived characters that the species shared with *Homo*, rather than on the primitive characters which it shared with *Australopithecus*. In this study there were also few characters linking *H. habilis* with *H. erectus* and *H. sapiens*: indeed, fewer synapomorphies were identified at Node E than at any other node on the cladogram (Table 5.03). *Homo sp.*, on the other hand, appears to be associated quite strongly with species of the genus *Australopithecus* (see synapomorphies at Nodes B and C: Table 5.03), and it cannot be placed parsimoniously as a member of the *Homo* clade (Figure 5.03).

Since there is still some uncertainty over the branching sequence of the hominid cladogram no recommendations are made here concerning possible changes in hominid nomenclature. There are, moreover, a variety of ways in which the present analysis might be improved, and thus either confirm or refute the pattern of relationships offered here. More characters, especially postcranial ones, could be included in the analysis and larger sample sizes might be possible as more fossils become available. The polarities of character state changes might be determined more reliably if the outgroup analysis were extended to include fossil hominoids, or if ontogenetic evidence were examined. The use of continuous rather than discrete character state data might improve the resolution of the method, as might the adoption of more complex parsimony methods that assign probabilities to individual character state changes (Felsenstein and Sober, 1986).

CHAPTER 6: STRATIGRAPHY AND GEOGRAPHICAL DISTRIBUTION

6.1 Stratigraphy of early *Homo*

6.2 Biogeography of early *Homo*

CHAPTER 6: STRATIGRAPHY AND GEOGRAPHICAL DISTRIBUTION

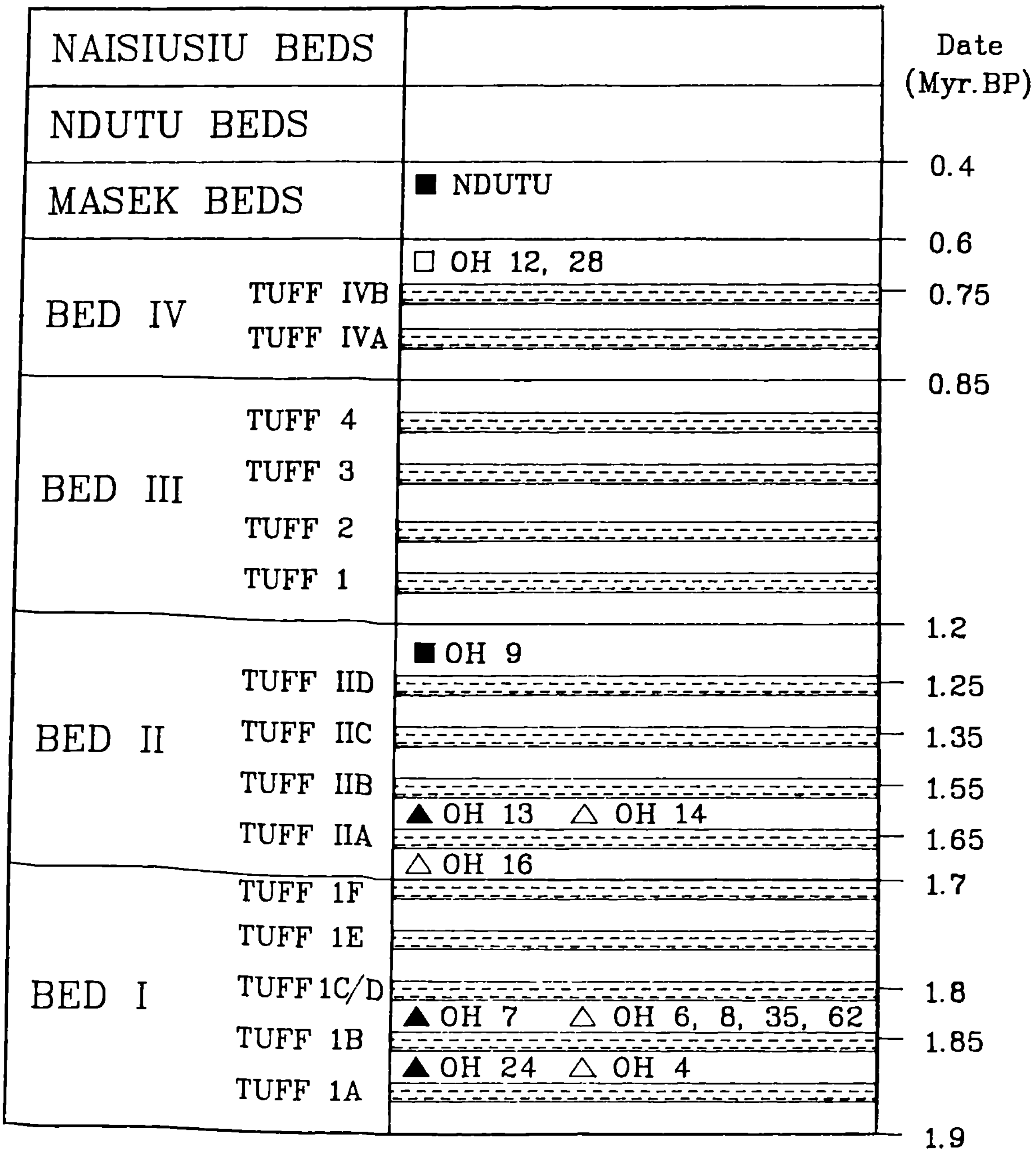
6.1 Stratigraphy of early Homo

6.1.1 The hominid sites

Olduvai Gorge

A synopsis of the stratigraphic succession at Olduvai Gorge is given in Figure 6.01 (stratigraphic information is from Hay, 1976; dating is taken from M.D. Leakey and Hay, 1982). This Figure also indicates the stratigraphic positions of some of the more important fossils that have been attributed to *H. habilis* and *H. erectus* (with the exception of OH 22, which is of uncertain geological provenience). According to Hay (1976: p. 129) OH 22 is "a surface find with a reddish-brown sandstone matrix characteristic of the eastern fluvial deposits", implying that the specimen was originally deposited in Bed III, or perhaps basal Bed IV. However, some Bed II strata are also reddish brown in colour, and the eastern fluvial deposits are known to contain clasts reworked from Bed II (Hay, 1976: p. 121). Harris and White (1979: p. 68) note that "Surface specimens from Olduvai are notorious for their frequently "derived" nature, such as stratigraphic displacement resulting from the condensed sequence ... and the steepness of the exposures". OH 22 was included in *H. habilis* in this study, and if the specimen really does come from Bed III deposits it is the only evidence for the survival of *H. habilis* later than Middle Bed II (about 1.6 Myr. B.P.).

Figure 6.01 Stratigraphic position of Olduvai hominids



KEY

■ H.erectus
(included in study)

□ H.erectus
(not in study)

▲ H.habilis
(included in study)

△ H.habilis
(not in study)

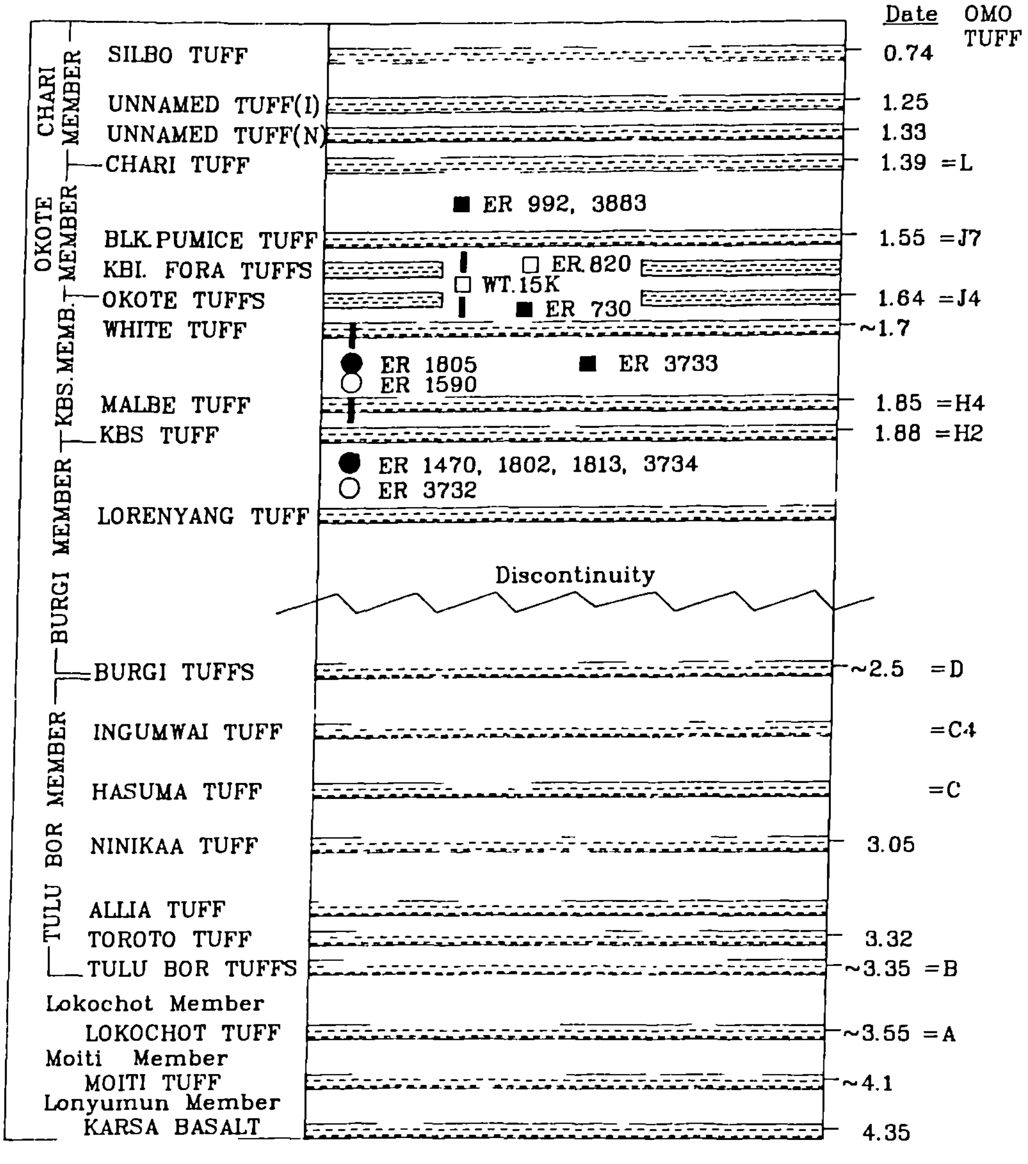
With the possible exception of OH 22, there appears to be no overlap in the temporal distribution of *H. habilis* and *H. erectus* at Olduvai Gorge. The earliest Olduvai specimen attributed to *H. erectus* is OH 9 (approximately 1.25 Myr. B.P.), and this species continues to be present in the vicinity of Olduvai Gorge (as indicated by the Ndutu cranium) until about 0.5 Myr. B.P.

Turkana Basin

The stratigraphy of the Koobi Fora region has been revised recently (Brown *et al.*, 1985a; Brown and Feibel, 1986), and dating and correlations with other sites are now firmly established (Brown *et al.*, 1985a; McDougall, 1985). Most of the specimens of early *Homo* recovered at Koobi Fora can now be located within the composite stratigraphic section (Figure 6.02). At this site there appears to be little overlap in the temporal distribution of the earlier species (*Homo sp.*) and the later species (*H. erectus*). The precise stratigraphic location of the ER 1805 skull is still uncertain, thus it is possible that *H. erectus* and *Homo sp.* were contemporaneous for a short period at Koobi Fora. The first appearance of *H. erectus* at Koobi Fora is in the KBS Member (revised stratigraphy), dated to between 1.7 and 1.8 Myr. B.P. *H. erectus* is well established in the Turkana region by 1.6 Myr. B.P., at a time when *H. habilis* is the only hominine species at Olduvai Gorge (Figure 6.01).

Revision of the dating of the Shungura Formation (Brown *et al.*, 1985a) has a bearing on the affinities of L.894-1, a fragmentary cranium from the lower Omo valley, Ethiopia, immediately to the north

Figure 6.02 Stratigraphic position of Turkana hominids



KEY

■ *H.erectus* (included in study)	● *Homo sp.* (included in study)
□ *H.erectus*	○ *Homo sp.*

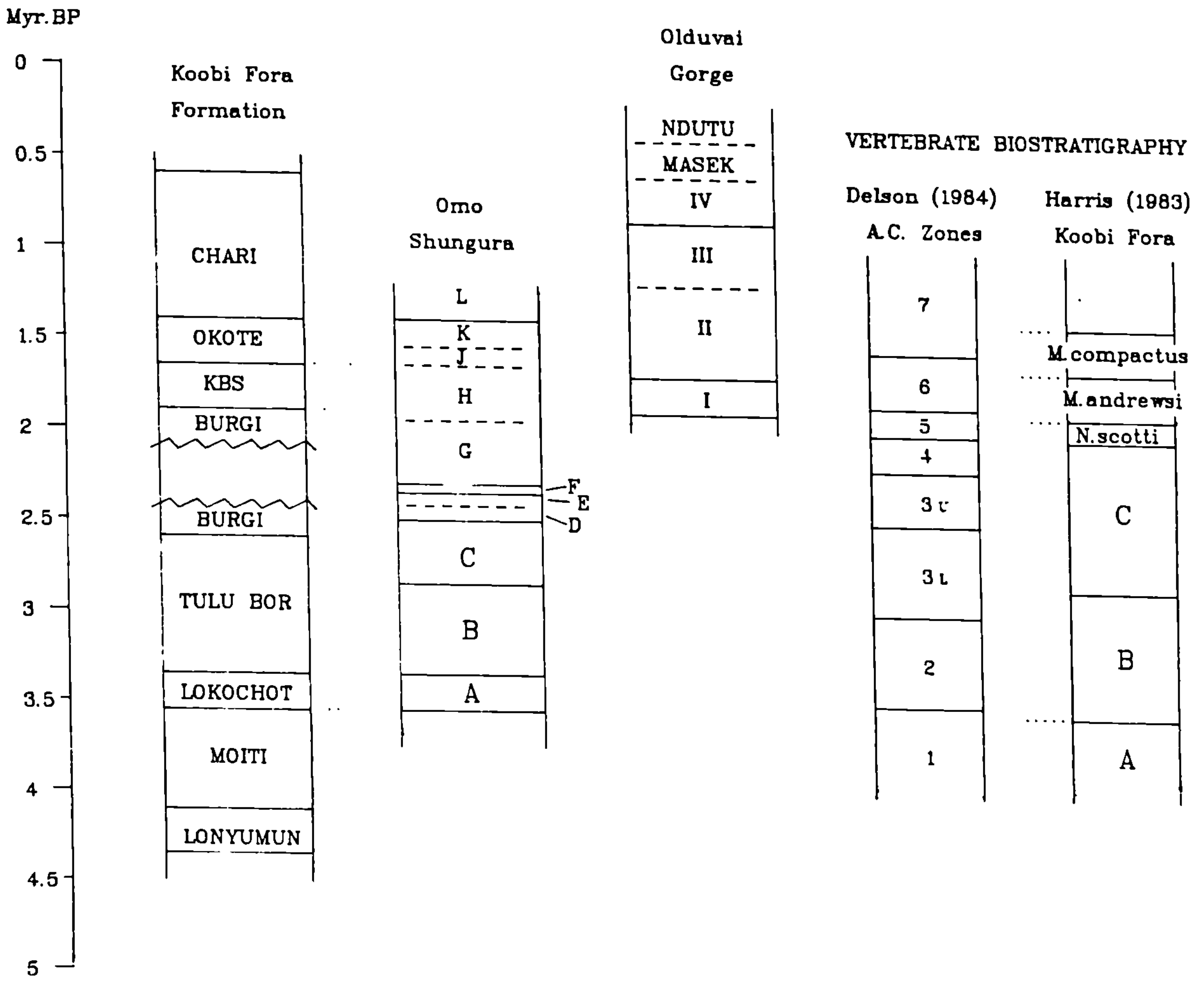
of Lake Turkana. This specimen, which was described as resembling *H. habilis*, was believed at the time of its discovery to be contemporaneous with the hominids of Bed I, Olduvai Gorge (Boaz and Howell, 1977). L.894-1 was recovered from Upper Member G deposits, and these strata are now considered to correlate with the upper part of the Burgi Member at Koobi Fora (Figure 6.03). Thus L.894-1 is probably contemporaneous with *Homo sp.*, rather than with *H. habilis*.

At a higher level in the Omo sequence another fragmentary cranium (L.P996-17) has been compared with *H. erectus* (Howell, 1978). This cranium was recovered from deposits towards the top of Member K, and the specimen is therefore contemporaneous with hominids such as ER 992 and ER 3883 from the upper part of the Okote Member at Koobi Fora (Figure 6.03).

South Africa

Two specimens of early *Homo* from sites in South Africa were assigned to *Homo sp.* in this study. These hominids were recovered from Sterkfontein Member 5 (Stw 53) and Swartkrans Member 1 (SK 847). In addition, an early *Homo* specimen from Swartkrans Member 2, lower component (SK15) was included in the comparative study, but was only very tentatively considered to belong to *Homo sp.*. The stratigraphy of the South African hominid sites has been reviewed by Vrba (1982) and Delson (1984). Radiometric dates and tephra correlations are not yet available for these sites, but some faunal correlations with dated East African sites have been established.

Figure 6.03 Correlation of East African early Homo sites



The suid and bovid species from Swartkrans Member 1 correspond to the fauna from Bed I to Middle Bed II at Olduvai Gorge and to the upper part of the KBS Member at Koobi Fora (White and Harris, 1977; Vrba, 1982; Harris, 1983). According to Delson (1984), however, the cercopithecids from Swartkrans Member 1 place these deposits "clearly" in Delson's African Cercopithecid Zone 5 (AC 5), which correlates with the Burgi Member at Koobi Fora and with upper Member G of the Omo Shungura Formation (Figure 6.03). Thus, on Delson's evidence, Swartkrans Member 1 predates all but the very earliest horizons at Olduvai Gorge.

Comparisons between the microfauna (Brain, 1982) and macrofauna (Vrba, 1982) of Swartkrans Member 1 and Sterkfontein Member 5 indicate that the latter site is contemporaneous *with, or slightly* later in time than the former. Delson (1984) places Sterkfontein Member 5 in AC 5 with Swartkrans Member 1, although he noted that Sterkfontein Member 5 has not yielded diagnostic Old World monkey fossils.

The assignment of SK 847 and Stw 53 to Homo sp. provides a further correlation between the two sites, and resolves a problem alluded to by Vrba (1982). The latter author accepted evidence that SK 847 was a more advanced hominid than Stw 53, which was at variance with the similar fauna and less advanced artefacts obtained from the Swartkrans site, compared to those from Sterkfontein Member 5. This anomaly between the hominids and the rest of the fauna disappears if SK 847 and Stw 53 are considered to be conspecific, as argued here.

The lower component of Member 2 at Swartkrans contains fossil remains of both A. robustus and Homo (Brain, 1982). Delson (1984) places this deposit at the top of (or even above) AC Zone 6, at a level equivalent to the Okote Member at Koobi Fora and to Bed II at Olduvai Gorge. However, Vrba (1982) suggested that a date closer to 1.0 Myr. B.P. is indicated by the bovid and suid evidence. Brain (1982) noted that it was possible that the hominid remains from Swartkrans Member 2 had been recycled from Member 1 deposits during an erosional episode.

6.1.2 Inter-site comparisons

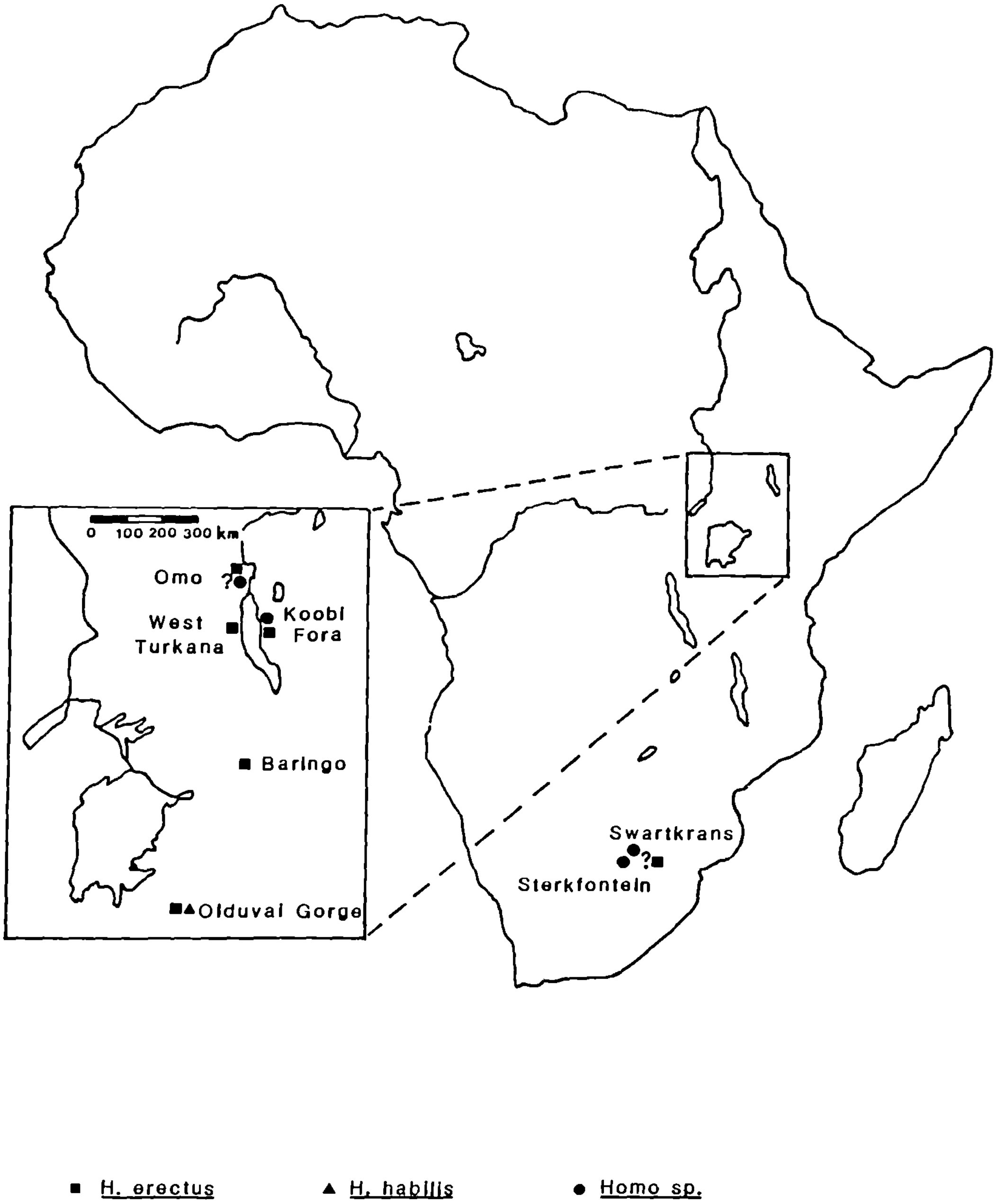
Figure 6.03 gives the chronological correlation between the composite stratigraphic sections of the Koobi Fora Formation, the Shungura Formation (Omo) and Olduvai Gorge. Also shown are the faunal zonations established by Harris (1983) at Koobi Fora, and by Delson (1984) for African cercopithecids. Dating information is taken from M.D. Leakey and Hay (1982) and Brown and Feibel (1986).

If Delson (1984) is correct in placing Swartkrans 1 and Sterkfontein 5 in AC Zone 5 (1.85 - 2.0 Myr. B.P.) then the presence of Homo sp. at these South African sites would be contemporaneous with the East African stratigraphic record of this species. Homo sp. appears to be absent at Olduvai Gorge, where the earliest strata only record the end of AC Zone 5. At Koobi Fora, however, Homo sp. is found in the upper part of the Burgi Member and the lower part of the KBS Member, strata which correlate with Delson's AC Zone 5 (Figure 6.03). The upper part of Member G of the Shungura Formation also correlates with this period, and I would thus expect the gracile hominids from Member G to represent *Homo sp.* rather than *H. habilis*.

There is some conflict between Delson's cercopithecid biostratigraphy and the bovid and suid comparisons of White and Harris (1977) and Vrba (1982). The latter studies imply younger dates for the South African sites, primarily because of faunal similarities to Bed II at Olduvai Gorge. However, the fossil record indicates that several faunal transitions occur later at Olduvai Gorge than at Koobi Fora. Harris (1983) noted that at Koobi Fora the replacement of *Metridiochoerus andrewsi* by *Metridiochoerus compactus* occurs towards the top of the Okote Tuff Complex (1.6 - 1.55 Myr. B.P.), whereas at Olduvai Gorge this change occurs at Tuff IIC (1.35 Myr. B.P.). Similar small discrepancies indicate that stages in the evolving *Kolpochoerus limnetes* lineage occur slightly later at Olduvai than at Koobi Fora. More substantial differences are seen in the stratigraphic record of subspecies of *Elephas recki* at the two sites (Harris, 1983). *E. recki ileretensis* first appears in the upper part of the KBS Member at Koobi Fora (approximately 1.7 - 1.6 Myr. B.P.), but is not found at Olduvai until Upper Bed II (1.35 - 1.2 Myr. B.P.). The succeeding subspecies *E. recki recki* appears in the Okote Member at Koobi Fora (1.6 - 1.4 Myr. B.P.), but only occurs in Bed III/IV at Olduvai (<1.2 Myr. B.P.).

Thus it would appear from the stratigraphic evidence that a late transition (or replacement) between *H. habilis* and *H. erectus* at Olduvai Gorge is consistent with the late arrival of some other fauna at this site. Harris (1983) suggested that ecological factors might explain some of the inter-site variation in faunal first-appearances, and it is notable that the Olduvai Gorge collections sample a single restricted sedimentary basin (Hay, 1976). Although it is possible that H. habilis is itself a late arrival at Olduvai Gorge (and might, therefore, have existed at an earlier period at other East African sites) there is, at present, no fossil evidence for such a conjecture. Furthermore, the delayed faunal transitions apparently only affect the post-Bed I fauna at Olduvai Gorge: Bed I fauna correlate with contemporaneous fauna at Koobi Fora and in the lower Omo valley.

Figure 6.04 African fossil sites with remains of early Homo



6.2 Biogeography of early Homo

6.2.1 Geographical distribution of early Homo

According to the results of this study, H. habilis fossils have been found only at Olduvai Gorge, which is the southernmost of a cluster of early Pleistocene hominid fossil sites in East Africa (Figure 6.04). There is no convincing evidence for this species at other African hominid sites. In the Turkana basin, approximately 1000 kilometres north of Olduvai Gorge, deposits contemporaneous with Olduvai Beds I and II yield fossils that resemble H. erectus. Penecontemporaneous cave deposits at Swartkrans and Sterkfontein in the Transvaal of South Africa contain fossils of Australopithecus robustus, Homo sp., and one fossil (SK 15) *which may* represent H. erectus. Thus H. habilis, in terms of its apparently restricted geographical distribution, is unlike H. erectus (which is widespread in East Africa and elsewhere) or Homo sp. (which appears to be present in both East and South Africa).

The South African hominid sites are geographically well-separated from those of East Africa, and different australopithecine species are found in the two regions: A. africanus and A. robustus occur in South Africa while A. afarensis and A. boisei are found in East Africa. One might also, therefore, expect to find a distinction between hominine groups in the two regions. There is some slight evidence that Homo sp. in East Africa is morphologically distinct from Homo sp. in South Africa (see metrical comparsions in Table 4.01 above), but such evidence is insufficient to maintain a species distinction between the two samples.

H. erectus is probably present at all of the East African fossil sites indicated on Figure 6.04. Additional fossil evidence for this species has been found at Melka Kunturé in Ethiopia (Chavaillon and Coppens, 1986), in Morocco and Algeria (Howell, 1978) and in Asia. Given the wide distribution of *H. erectus*, this species might well be expected to appear in the South African fossil record. However, no diagnostic remains of *H. erectus* have been recovered at the South African sites, although it is possible that the SK 15 mandible belongs to *H. erectus* rather than to *Homo sp.*

6.2.2 Sympatry with *Australopithecus*

All three species of 'early' *Homo* (*H. habilis*, *Homo sp.* and *H. erectus*) appear to have existed in sympatry with 'robust' australopithecines (*A. robustus* and *A. boisei*). *A. robustus* occurs at fossil sites in South Africa which have been dated faunally to between 2.0 and 1.5 Myr. B.P. (Delson, 1984). At Swartkrans Member 1, *A. robustus* is sympatric with hominids assigned here to *Homo sp.*, while in Member 2 the australopithecine is sympatric either with *Homo sp.*, or possibly with *H. erectus*. The few hominids found at Kromdraai in South Africa have been attributed to *A. robustus*, but remains of *Homo* have not yet been recovered from this site (Vrba, 1981).

A. boisei has a fossil record at Olduvai Gorge from 1.8 to 1.2 Myr. B.P. (M.D. Leakey and Hay, 1982) and is thus sympatric with

H. habilis (but probably not *H. erectus*) at this site. At hominid sites in the Turkana Basin, *A. boisei* is sympatric with both *Homo sp.* and with *H. erectus*. At Koobi Fora *A. boisei* occurs from the upper part of the Burgi Member to the upper part of the Okote Member (approximately 2.0 to 1.4 Myr. B.P.), but earlier dates of around 2.5 Myr. B.P. are reported for some hominids, attributed to *A. boisei*, from West Turkana (Walker *et al.*, 1986).

In the phylogenetic analysis (Chapter 5), *Homo sp.* was most parsimoniously placed as the sister taxon of the 'robust' australopithecines. If the 2.5 Myr. B.P. West Turkana hominids represent belong to the 'robust' australopithecine clade, then *Homo sp.* must have had a lineage separate from other hominids at least 2.5 Myr. B.P. An alternative interpretation of the West Turkana 'robust' australopithecines views tham as a distinct species of *Australopithecus* (Delson, 1987), whose cladistic affinities await detailed examination.

CHAPTER 7: DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

7.1 Assessment of methods of analysis

7.2 Assessment of results

CHAPTER 7: DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

7.1 Assessment of methods of analysis

7.1.1 Size removal and quantification of characters

Summary of method

In this study morphological characters were quantified in a way which reflects, in part, traditional systematic practice. Systematicists often compare organisms of different overall size on a character-by character basis, after implicitly scaling the organisms to the same overall size. When comparing particular characters in two organisms, the absolute size of any given morphological structure is also taken into account, so that (for example) the evidence from small differences in the absolute size of dental structures can be weighed against larger absolute differences in external cranial dimensions.

Overall size can be regarded as a single morphological character. However, while it is of doubtful value in phylogenetic analysis, overall size which has a profound effect (through covariation and allometry) on all other metric characters. The fact that size can increase or decrease in an evolutionary lineage, and that sources of intraspecific variation in size are manifold, must render overall size *per se* of only marginal value in a systematic study. Therefore, the isometric effect of overall size was removed *ab initio* in this analysis by scaling each form to a standard size. Having removed the effect of overall size, the individual characters were made comparable with each other by a further scaling process. In effect, each character was expressed as a ratio, using a 'standard'character value as the ratio denominator. The resulting ratio, after logarithmic transformation, indicates the amount by which the character is proportionately larger or smaller than the same character measured on the 'standard' animal.

Advantages and disadvantages

In principle, the method adopted here can be applied to any group of organisms that share a number of measurable homologous structures. For two forms to be compared by this method there needs only to be a set of measurements of different anatomical structures that can be obtained on each of the two forms. The method requires that both small (e.g. dental) and large (e.g. external cranial) dimensions are included in the measurement set, to ensure an adquate range of Q-mode variation. Among mammals, the method is probably applicable to taxonomic categories up to the family or superfamily level, and is particularly applicable to fossil groups since individuals with missing data values can nonetheless be included in the analysis.

In the present study the characters were not specially selected with this particular size-removal method in mind. The analytical procedure might have been facilitated by extending the Q-mode range, i.e. by including measurements that were either larger or smaller than the existing set of measurements. Clearly, for cranial material no measurements larger than the maximum cranial dimensions are obtainable (unless larger composite measurements are computed by successive addition of smaller measurements). However, there is no theoretical lower limit below which smaller measurements cannot be taken, although in practice the effects of overall size do not extend below the cellular level (cells are of the same size in the mouse and in the elephant). Thus the practical lower limit for measurement would only be encountered at microscopic dimensions, at or above the dimensions of individual cells.

The method as used here does, however, require homologous points to be identified on each form to be compared. This can be problematic because some structures (e.g. the supraorbital torus) have few, if any, definable homologous points, although the structure as a whole may be homologous between different forms. The emphasis on homologous landmarks also restricts the method to low taxonomic levels (this restriction is reinforced by the necessity to adopt a 'standard' that is morphologically intermediate between the forms under investigation). The method should be viewed as a means of sampling morphological deviation from a standard, rather than one of reproducing, in measurements, a complete organism.

7.1.2 Comparisons within and between species

After transforming characters into size-independent 'shape' variables, a non-parametric measure of morphological distance - Mean Character Difference (MCD) - was used to make quantitative comparisons between individual fossils. The ranges of variation in MCD in small samples of extant primate species were used as a guide to the expected maximum range of variation in species of fossil hominid. A moderately consistent upper limit to intraspecific values of between-individual MCD had been determined in several extant primate species, even though those species exhibited considerable variation in body size and in level of sexual dimorphism in size. This empirically-determined limit for intraspecific MCD in extant primates was applied to conventionally-defined fossil hominid species, with a view to assessing shape variation in those species.

It could be argued that variation in extant species is an inadequate guide to the amount of variation expected in fossil species. According to the tenets of phyletic gradualism, fossil species vary in time, as well as exhibiting the spatial and individual variation seen in extant species. My view is that if a fossil species varies in time, to a degree that increases its variation beyond that characteristic of an extant species, then it is useful to recognise the additional variation by invoking a taxonomic distinction between the earlier and later forms of the species. In this study, H. erectus was subdivided into African and Asian samples which are temporally, as well as geographically distinct. The two samples appeared as sister taxa on the overall cladogram, and it is quite possible that the earlier form is ancestral to the latter.

Hominid palaeontologists have frequently resorted to the extant primates as a source of models for morphological variation in hominid species. It may, therefore, come as no surprise that most of the conventionally-defined hominid species included in the present study appeared to exhibit variation that is consistent with that seen in the primates. I find little hard evidence for the assertion by Tattersall (1986) that palaeontologists are likely to have underestimated species diversity in the hominid fossil record. Although I have found grounds for subdividing 'early' Homo, this was clearly a problematic taxon that was widely suspected to contain the remains of more than one species. Tattersall (1986) finds theoretical support for his argument in the fact that "closely related primate species show only minor morphological differences from one another, sometimes in parts of the anatomy that do not preserve in the fossil record". I counter this argument by suggesting that closely-related, morphologically-similar primates are rarely found in sympatry, and would equally rarely enter the same geological deposit as fossils. Such sibling species might be found at different, geographically-separated sites (or at different horizons within the same site), and there is thus good reason for circumspection before aggregating site samples, or samples from widely separated stratigraphic levels.

There are some alternatives to the use of maximal intraspecific variation as a guide to defining fossil species. One can seek to identify morphological discontinuities that have arisen between species: such discontinuities are to be expected, both from the unique nature of adaptive evolution and as a consequence of genetic drift following the reproductive isolation of a species from its parent stock. The principal counter-arguments to the use of discontinuity as a marker for species boundaries are that discontinuities may not be discernible between anagenetically-related species, and that other sources of discontinuity (e.g. interruption in sedimentation, intraspecific dimorphism) may mimic interspecific differences.

Another method of recognising species (and one that has been advocated by cladists, including Bonde (1981), Andrews (1984) and Tattersall (1986)) is to identify the unique specialisations, or autapomorphies, that characterise each terminal taxon. It is important to recognise that this amounts to a relative, rather than an absolute, definition of the species. Autapomorphies can only be identified in relation to the phylogeny for the wider taxonomic group to which the species in question belongs. This is put cogently by Bonde: "To identify a species or propose a new one amounts to hypothesise a phylogenetic relationship" (Bonde, 1981, p. 32).

7.1.3 Phylogenetic analysis

Summary of method

The same character state information which was used to make phenetic comparisons between individuals and groups, was also used to determine the most parsimonious hominid cladogram. The calculations were carried out with a computer program (PAUP) which determines the minimum length bifurcating network (Wagner tree) for a given character state matrix. In this study the character states for each character were ordered, and thus constituted a morphocline. The PAUP program assumes that changes in either direction along a morphocline are equally probable. It also assumes that a change, for example, from state 3 to state 5 implies evolution through the intermediate state 4, and thus is counted as two evolutionary steps.

Unlike traditional cladistic analysis, this version of numerical cladistics does not require the prior determination of character state polarity. However, in order to produce a cladogram the minimum length Wagner tree must be 'rooted', and this is equivalent to declaring a set of character states (those that characterise the root) to be primitive. In this study the Wagner tree was rooted by including a hypothetical ancestral taxon, assumed to possess only primitive character states, in the maximum parsimony analysis. The character states for the hypothetical ancestor were determined by an outgroup analysis that took advantage of previous knowledge of outgroup structure. The most parsmonious Wagner tree for the ingroup taxa (hominids) was then rooted, to form a cladogram, by placing the hypothetical ancestor as the sister group of the hominids.

Alternative assumptions

Most methods of phylogenetic reconstruction embody assumptions about possible character state change, and these assumptions in turn are often chosen from a variety of possible options. In selecting a particular cladistic method one may, in fact, influence the outcome of the analysis. The principal options exercised here concern parsimony criteria, polarity determination and character weighting.

The calculation of the minimum length tree automatically minimises homoplasy, in so far as the latter can be defined as the independent appearance on the tree of a given character state. The maximum parsimony criterion, however, makes no distinction between the relative probabilities of character convergence and character reversal: both forms of homoplasy are equally likely on the resultant cladogram. In using the PAUP program all changes between adjacent character states were considered equally probable, and no weighting was attached to particular characters, or to particular changes of state within a given character. PAUP does provide an option that takes account of the different number of character states assigned to each character, but selecting this option had little effect on the outcome of the present study.

Perhaps the greatest element of uncertainty in a cladistic analysis surrounds the determination of ancestral character states. Four methods of polarity determination are worthy of consideration, these being 'commonality', 'ontogeny', 'functional morphology' and 'stratigraphy' (Stevens, 1980; Bishop, 1982). Outgroup analysis is the preferred version of the commonality method. The assumption underlying outgroup analysis is that character states that are primitive for the ingroup are to be found among the ingroup's successive sister taxa. The ontogenetic method invokes von Baer's principle in seeking changes from primitive to derived character states among the ingroup ontogenies (Bonde, 1984). The argument from functional morphology equates functional and ecological specialisation with the derived pole of a given character state morphocline, while the stratigraphic method uses the temporal distribution of character states in the fossil record to construct a 'chronocline', whose polarity is implicit.

The ontogenetic method of polarity determination is considered reliable, although it may be confounded in instances of neoteny when a descendant species exhibits the primitive ontogeny (Bonde, 1984). The method was eschewed here solely because of the paucity of ontogenetic information for fossil hominids. Ontogenetic information _is_ available for modern humans, but the latter are perhaps more likely to exhibit neoteny than are their fossil relatives.

The justification for using functional morphology to identify homologies and determine polarity has been reviewed in detail by Bonde (1983), who found little to recommend it. Bonde (1983) pointed out that functional and non-functional characters are probably of equal value in phylogeny reconstruction. He also suggested that there is a role for functional analysis in the initial selection of characters: "A functional analysis may also show which features are completely interdependent in a functional complex, and therefore presumably might count as only one phylogenetic argument" (Bonde, 1983, p. 18).

Likewise, although stratigraphic information has an important role in the conversion of a cladogram into a phylogenetic tree (for example, in establishing the minimum age of a clade), its use in building the initial clade must be viewed with caution (Bonde, 1977). Although morphological characters must, by definition, evolve in the sequence primitive to derived, the fossil species that preserve those characters can appear in almost any sequence in the fossil record

(Vrba (1980) provides a good example of this phenomenon in the evolution of mandibular morphology among Alcelaphines). Fortuitously, in the analysis presented in Chapter 5 above, the order of appearance of the hominid clades is partially reflected in the stratigraphic sequence of fossils, in that, for example, A. afarensis is both the earliest and the most primitive hominid.

7.2 Assessment of results

7.2.1 Fulfillment of the aims of the study

The declared aims of this study were to test whether the current extended hypodigm of *H. habilis* represents a single, species-level taxon; to examine the distinctiveness of this species when compared to other species of hominid, and to assess the phylogenetic relationships between *H. habilis* and other species of the genera *Homo* and *Australopithecus*. Fossils attributed to *H. habilis* were found to be too variable in morphology to justify their retention in a single species. Therefore *H. habilis* was partitioned, on 'shape' criteria, into *H. habilis* s.s. (sensu stricto, known only from Olduvai Gorge) and *Homo sp.*, represented by fossils from Koobi Fora and sites in South Africa. The shape differences which support this subdivision were found among both crania and mandibles of the extended hypodigm, and are of a degree characteristic of the variation seen between, rather than within, extant primate species. Size variation in *H. habilis* s.s. appears to be on a par with that observed among non-dimorphic extant primates, but *Homo sp.* exhibits size variation comparable with that seen in *Papio*, the most sexually dimorphic primate included in the study.

The results of this study indicate that *H. habilis* s.s. is further differentiated from *Homo sp.* in several characters of the cranial base, by the possession of a thinner cranial vault, shorter parietal, narrower biorbital breadth, smaller palate and mandible, mesiodistally-elongated cheek teeth, narrower P_3 and larger incisors (all characters relative, not absolute). Additional characters distinguishing *H. habilis* s.s. from *Homo sp.* can be found in the original species diagnosis (L.S.B. Leakey *et al.*, 1964) and in some studies of hominid dental crown morphology (e.g. Groves and Mazak, 1975; Wood *et al.*, 1983, Fig. 8).

Cladistic analysis throws further light on the morphological distinction between *H. habilis* s.s. and *Homo sp*. The former species is most parsimoniously interpreted as a relatively primitive hominid, which nonetheless shares a few derived characters with *H. erectus* and *H. sapiens*. *Homo sp.*, on the other hand, is linked by several derived characters to the 'robust' australopithecines. The *Homo sp.*/ 'robust' australopithecine clade in turn is linked cladistically with *A. africanus*, providing several more characters shared between *Homo sp.* and species of *Australopithecus*. The 'primitive' nature of *H. habilis* s.s. is supported by interpretations of Olduvai Bed I hominid postcrania (Napier, 1962; Davis, 1964; Lewis, 1973, 1981), and by preliminary reports of postcranial elements recently recovered from that site (Johanson *et al.*, 1987). The postcrania of *Homo sp.* is unknown, but postcranial elements from the upper part of the Burgi Member at Koobi Fora (which are contemporaneous with the known crania of *Homo sp.*) appear to differ morphologically from those postcrania of *H. erectus* and *H. habilis* that have been described by Brown *et al.* (1985b) and Johanson *et al.* (1987) respectively.

7.2.2 Recommendations for further work

The suggested distinction between H. habilis and Homo sp. deserves further investigation. In particular, more detailed examination of the cranial, mandibular and dental material studied here may yield additional characters in which these hominids can be distinguished. The morphology of the postcrania may also differ in the two groups. Both of the major sites at which these hominids have been found - Koobi Fora and Olduvai Gorge - continue to be productive of hominid fossils, and an analysis of the enlarged collections will allow the taxonomic distinctions raised in the present study to be confirmed or refuted.

The method of morphological comparison adopted in this study can be improved by careful selection and definition of the measurement set, with the aim of reducing the proportion of missing data and extending the range of measurements to include microscopic dimensions. It might also prove valuable to examine the utility of the method in investigating other primate and non-primate mammalian groups. The cladistic analysis might be improved by including postcranial characters and by considering ontogenetic data where such information is available. Inclusion of Miocene hominoids in the outgroup analysis could also be considered as a way of generating more accurate estimates of the ancestral hominid morphotype.

REFERENCES

Abbott SA (1984) A comparative study of tooth root morphology in the great apes, modern man and early hominids. Ph.D. Thesis, University of London.

Aguirre E (1970) Identificacion de "Paranthropus" en Makapansgat. Crônical del XI Congresso Nacional de Arqueologia, Merida, 1969: 98-124.

Albrecht GH (1976) Methodological approaches to morphological variation in primate populations: the Celebesian macaques. Yearbook of Physical Anthropology 20: 290-308

Albrecht GH (1978) Some comments on the use of ratios. Systematic Zoology 27: 67-71.

Andrews P (1978) Taxonomy and relationships of fossil apes. In Chivers DJ and Joysey KA (eds.) Recent advances in primatology. Volume 3. Evolution. London, Academic: 43-56.

Andrews P (1984) An alternative interpretation of the characters used to define Homo erectus. Courier Forschungsinstitut Senckenberg #69: 167-175.

Andrews P (1986) Catarrhine evolution. In Wood BA et al. (eds.) Major topics in primate and human evolution. Cambridge, Cambridge University Press: 107-129.

Andrews P and Cronin JE (1982) The relationships of Sivapithecus and Ramapithecus and the evolution of the orang-utan. Nature 297: 541- 546.

Arambourg C and Coppens Y (1967) Sur la découverte dans le Pléistocéne Inferieur de la vallée de l'Omo (Ethiopie) d'une mandibule d'australopithécien. Comptes Rendus des séances de l'Académie des Sciences D 265: 589-590.

Archibald JD et al. (1972) Implications of relative robusticity in the Olduvai metatarsals. American Journal of Physical Anthropology 37: 93-95.

Arnold EN (1981) Estimating phylogenies at low taxonomic levels. Zeitschrift für Zoologische Systematik und Evolutionsforschung 19: 1-35.

Ashton EH et al. (1957) The descriptive use of discriminant functions in physical anthropology. Proceedings of the Zoological Society of London, B, 146: 552-572.

Atchley WR (1978) Ratios, regression intercepts, and the scaling of data. Systematic Zoology 27: 78-83.

Atchley WR et al. (1976) Statistical properties of ratios. I. Empirical results. Systematic Zoology 25: 137-148.

Atkinson AC (1985) Plots, transformations and regression: an introduction to graphical methods of diagnostic regression analysis. Oxford, Clarendon Press.

Babin C (1980) Elements of palaeontology. Chichester, Wiley.

Behrensmeyer AK and Laporte LF (1981) Footprints of a Pleistocene hominid in northern Kenya. Nature 289: 167-169

Berge C and Kazmierczak J-B (1986) Effects of size and locomotor adaptations on the hominid pelvis: evaluation of australopithecine bipedality with a new multivariate method. Folia Primatologica 46: 185-204.

Berry RJ (1979) Genes and skeletons - ancient and modern. Journal of Human Evolution 8: 669-677.

Beynon AD and Wood BA (1986) Variations in enamel thickness and structure in East African hominids. American Journal of Physical Anthropology 70: 177-193.

Bielicki W (1966) On "Homo habilis". Current Anthropology 7: 576-577.

Bilsborough A (1972) Cranial morphology of neanderthal man. Nature 237: 351-352.

Bilsborough A (1973) A multivariate study of evolutionary change in the hominid cranial vault and some evolution rates. Journal of Human Evolution 2: 387-403.

Bilsborough A (1976) Patterns of evolution in Middle Pleistocene hominids. Journal of Human Evolution 5: 423-439.

Bilsborough A (1984) Multivariate analysis and cranial diversity in Plio-Pleistocene hominids. In Van Vark GN and Howells WW (eds.) Multivariate statistical *methods in* physical anthropology. Dordrecht, Reidel: 351-375.

Bilsborough AD and Wood BA (n.d.) Cranial morphology of early hominids. I. Facial region. American Journal of Physical Anthropology (submitted).

Bishop MJ (1982) Criteria for determining the direction of character state changes. Zoological Journal of the Linnean Society 74: 197-206.

Bishop MJ and Friday AE (1985) Evolutionary trees for nucleic acid and protein sequences. Proceedings of the Royal Society of London 226B: 271-302.

Bishop WW (ed.) (1978) Geological background to fossil man. Edinburgh, Scottish Academic Press.

Black D (1927) On a lower molar hominid tooth from the Chou Kou Tien deposit. Palaeontologia Sinica (D) 7: 1-29.

Blackith RE and Reyment RA (1971) Multivariate morphometrics. London, Academic Press.

Boaz NT and Howell FC (1977) A gracile hominid cranium from Upper Member G of the Shungura Formation, Ethiopia. American Journal of Physical Anthropology 46: 93-108.

Bonde N (1976) Nyt om menneskets udviklingshistorie. Dansk geol Forening Arsskr.f. 19-34.

Bonde N (1977) Cladistic classification as applied to vertebrates. In Hecht MK et al. (eds.) Major patterns in vertebrate evolution. New York, Plenum: 741-804.

Bonde N (1981) Problems of species concepts in palaeontology. Proceedings, International symposium on concepts and methods in paleontology, Barcelona: 19-34.

Bonde N (1983) Functional anatomy and reconstruction of phylogeny. In Buffetaut E et al. (eds.) Actes du Symposium Paléontologique Georges Cuvier: 11-26.

Bonde N (1984) Primitive features and ontogeny in phylogenetic reconstructions. Videnskabelige Meddelelser fra Dansk Naturhistorik Forening i Kjøbenhavn 145: 219-236.

Boyce AJ (1969) Mapping diversity: a comparative study of some multivariate methods. In Cole AJ (ed.) Numerical taxonomy. London, Academic Press: 1-31.

Brace CL (1967) The stages of human evolution: human and cultural origins. Englewood Cliffs, Prentice Hall.

Brace CL (1981) Tales of the phylogenetic woods: the evolution and significance of evolutionary trees. Yearbook of Physical Anthropology 56: 411-429.

Brace CL et al. (1972) Tooth measurements and the rejection of the taxon "Homo habilis". Yearbook of Physical Anthropology 16: 50-68.

Brain CK (1967) The Transvaal Museum's fossil project at Swartkrans. South African Journal of Science 63: 378-384.

Brain CK (1970) New finds at the Swartkrans australopithecine site. Nature 225: 1112-1119.

Brain CK (1982) The Swartkrans site: stratigraphy of the fossil hominids and a reconstruction of the environment of early Homo. Prétirage, Premier Congrés International de Paléontologie Humain. Paris, CNRS: 676-706.

Brain CK *et al.* (1974) A new hominid innominate bone from Swartkrans. Annals of the Transvaal Museum *29*: 55-63.

Bräuer G (1984) A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In Smith FH and Spencer F (eds.) The origins of modern humans: a world survey of the fossil evidence. New York, Liss: 327-410.

Bräuer G and Leakey RE (1986) The ES-11693 cranium from Eliye Springs, West Turkana. Journal of Human Evolution *15*: 289-312.

Bronowski J and Long WM (1951) Statistical methods in anthropology. Nature *168*: 794-795.

Broom R (1937) The Sterkfontein ape. Nature *139*: 326.

Broom R (1938) The Pleistocene anthropoid apes of South Africa. Nature *142*: 377-379.

Broom R and Robinson JT (1949) A new type of fossil man. Nature *164*: 322-323.

Broom R and Robinson JT (1952) Swartkrans ape-man, *Paranthropus crassidens*. Transvaal Museum Memoirs *6*: 1-124.

Brothwell DR (1981) Digging up bones. 3rd Edition. Oxford, Oxford University Press.

Brown FH and Feibel (1986) Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. Journal of the Geological Society of London *143*: 297-310.

Brown FH *et al.* (1985a) An integrated Plio-Pleistocene chronology for the Turkana Basin. In Delson E (ed.) Ancestors: the hard evidence. New York, Liss: 82-90.

Brown F *et al.* (1985b) Early *Homo erectus* skeleton from west Lake Turkana, Kenya. Nature *316*: 788-792.

Buffon G-LL (1749) Histoire naturelle, générale et particuliere. Paris, Imprimerie Royale.

Cain AJ and Harrison GA (1958) An analysis of the taxonomist's judgement of affinity. Proceedings of the Zoological Society of London *131*: 85-98.

Cain AJ and Harrison GA (1960) Phyletic weighting. Proceedings of the Zoological Society of London *135*: 1-31.

Campbell BG (1964) Just another man-ape? Discovery *25*(6): 37-38.

Campbell BG (1978) Some problems in hominid classification and nomenclature. In Jolly CJ (ed.) Early hominids of Africa.

London, Duckworth: 567-581.

Campbell NA (1978) Multivariate analysis in biological anthropology: some further considerations. Journal of Human Evolution 7: 197-203.

Chamberlain AT and Wood BA (1985) A reappraisal of variation in hominid mandibular corpus dimensions. American Journal of Physical Anthropology 66: 399-405.

Chamberlain AT and Wood BA (in press) Early hominid phylogeny. Journal of Human Evolution.

Chavaillon J and Coppens Y (1986) Nouvelle découverte d'Homo erectus à Melka Kunturé (Ethiopie). Comptes Rendus des séances de l' Académie des Sciences II 303: 99-104.

Cherry LM et al. (1982) Body shape metrics and organismal evolution. Evolution 38: 914-933.

Cheverud JM (1982) Phenotypic, genetic and environmental integration in the cranium. Evolution 36: 499-516.

Cheverud JM and Richtsmeier JT (1986) Finite element scaling applied to sexual dimorphism in the rhesus macaque (Macaca mulatta) facial growth. Systematic Zoology 35: 381-399.

Cheverud JM et al. (1983) The measurement of form and variation in form in an application of three-dimensional quantitative morphology by finite-element methods. American Journal of Physical Anthropology 62: 151-165.

Ciochon RL (1983) Hominoid cladistics and the ancestry of modern apes and humans. A summary statement. In Ciochon RL and Corruccini RS (eds.) New interpretations in ape and human ancestry. New York, Plenum: 783-843.

Ciochon RL and Corruccini RS (1976) Shoulder joint of Sterkfontein Australopithecus. South African Journal of Science 72: 80-82.

Ciochon RL and Corruccini RS (eds.) (1983) New interpretations in ape and human ancestry. New York, Academic Press.

Clark GA (1980) Multivariate analysis of "Telanthropus capensis": implications for hominid sympatry in South Africa. Quaternaria 22: 39-64.

Clarke RJ (1977) A juvenile cranium and some adult teeth of early Homo from Swartkrans, Transvaal. South African Journal of Science 73: 46-49.

Clarke RJ and Howell FC (1972) Affinities of the Swartkrans 847 hominid cranium. American Journal of Physical Anthropology 37: 319-336.

Clarke RJ et al. (1970) More evidence of an advanced hominid at Swartkrans. Nature 225: 1219-1222.

Clutton-Brock TH et al. (1977) Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature 269: 797-800.

Coppens Y (1970) Les restes d'Hominides des series inferieures et moyennes des formations plio-villafranchiennes de l'Omo en Ethiopie. Comptes Rendus des séances de l'Académie des Sciences D 271: 2286-2289.

Coppens Y (1971) Les restes d'Hominides des series superieures des formations plio-villafranchiennes de l'Omo en Ethiopie. Comptes Rendus des séances de l' Académie des Sciences D 272: 36-39.

Corruccini RS (1973) Size and shape in similarity coefficients based on metrical characters. American Journal of Physical Anthropology 38: 743-754.

Corruccini RS (1974) Calvarial shape relationships between fossil hominids. Yearbook of Physical Anthropology 18: 89-109.

Corruccini RS (1975a) Multivariate analysis in biological anthropology: some considerations. Journal of Human Evolution 4: 1-19.

Corruccini RS (1975b) Metrical analysis of Fontéchevade II. American Journal of Physical Anthropology 42: 95-98.

Corruccini RS (1976) Multivariate allometry and australopithecine variation. Evolution 30: 558-563.

Corruccini RS (1977a) Correlation properties of morphometric ratios. Systematic Zoology 26: 211-214.

Corruccini RS (1977b) Crown component variation in hominoid lower third molars. Zeitschrift für Morphologie und Anthropologie 68: 14-25.

Corruccini RS and Ciochon RL (1979) Primate facial allometry and interpretations of australopithecine variation. Nature 281: 62-64.

Corruccini RS and McHenry HM (1980) Cladometric analysis of Pliocene hominids. Journal of Human Evolution 9: 209-221.

Creel N (1986) Size and phylogeny in hominoid primates. Systematic Zoology 35: 81-99.

Cronin JE et al. (1981) Tempo and mode in human evolution. Nature 292: 113-122.

Cuvier G (1863) The animal kingdom according to its organisation. London, Bohn.

Davis PR (1964) Hominid fossils from Bed I, Olduvai Gorge, Tanganyika. A tibia and fibula. Nature 201: 967-970.

Day MH (1967) Olduvai hominid 10: a multivariate analysis. Nature 215: 323-324.

Day MH (1971) Postcranial remains of *Homo erectus* from Bed IV, Olduvai Gorge. Nature 232: 383-387.

Day MH (1986a) Bipedalism: pressures, origins and modes. In Wood BA *et al.* (eds.) Major topics in primate and human evolution. Cambridge, Cambridge University Press: 188-202.

Day MH (1986b) Guide to fossil man. 4th Edition. London, Cassell.

Day MH and Leakey REF (1973) New evidence of the genus *Homo* from East Rudolf, Kenya. I. American Journal of Physical Anthropology 39: 341-354.

Day MH and Leakey REF (1974) New evidence of the genus *Homo* from East Rudolf, Kenya. III. American Journal of Physical Anthropology 41: 367-380.

Day MH and Napier JR (1964) Hominid fossils from Bed I, Olduvai Gorge, Tanganyika. Fossil foot bones. Nature 201: 967-970.

Day MH and Wood BA (1968) Functional affinities of the Olduvai Hominid 8 talus. Man 3: 440-45.

Day MH *et al.* (1975) New hominids from East Rudolf, Kenya, I. American Journal of Physical Anthropology 42: 461-476.

Day MH *et al.* (1976) New hominids from East Turkana, Kenya. American Journal of Physical Anthropology 45: 369-436.

Dean MC (1986) *Homo* and *Paranthropus*: similarities in the cranial base and developing dentition. In Wood BA *et al.* (eds.) Major topics in primate and human evolution. Cambridge, Cambridge University Press: 249-265.

Dean MC and Wood BA (1981) Metrical analysis of the basicranium of extant hominoids and *Australopithecus*. American Journal of Physical Anthropology 54: 63-71.

Dean MC and Wood BA (1982) Basicranial anatomy of Plio-Pleistocene hominids from East and South Africa. American Journal of Physical Anthropology 59: 157-174.

Dean MC and Wood BA (1984) Phylogeny, neoteny and growth of the cranial base in hominoids. Folia Primatologica 43: 157-180.

De Bonis, L. (1983) Phyletic relationships of Miocene hominoids and higher primate classification. In Ciochon RL and Corruccini RS (eds.) New interpretations in ape and human ancestry. New York, Plenum: 625-649.

Delson E (1984) Cercopithecid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. Courier Forschungsinstitut Senckenberg #69: 199-218.

Delson E (1986) Human phylogeny revised again. Nature 322: 496-497.

Delson E (1987) Evolution and palaeobiology of robust australopithecines. Nature 327: 654-655.

Delson E et al. (1977) Reconstruction of hominid phylogeny: a testable framework based on cladistic analysis. Journal of Human Evolution 6: 263-278.

De Lumley H and De Lumley M-A (1971) Découverte de restes humains anténéandertaliens datés du début de Riss à la Caune de l'Arago (Tautavel, Pyrénées-Orientales). Compte Rendus des Séances de l'Académie de Sciences 272: 1729-1742.

De Villiers H (1968) The skull of the South African Negro. A biometrical and morphological study. Johannesburg, University of the Witwatersrand Press.

Dobzhansky T et al. (1977) Evolution. San Francisco, Freeman.

Dodson P (1978) On the use of ratios in growth studies. Systematic Zoology 27: 62-67.

Dubois E (1894) Pithecanthropus erectus, eine menschenaehnliche Ubergangsforme aus Java. Batavia, Landesdruckerie.

Editorial (1971) Confusion over fossil man. Nature 232: 294-295.

Editorial (1973) More questions than answers at East Rudolf. Nature 242: 431.

Editorial (1974) Should fossil hominids be reclassified? Nature 248: 635.

Editorial (1976) Important fossil skull found at Sterkfontein. South African Journal of Science 72: 227.

Eldredge N and Cracraft J (1980) Phylogenetic patterns and the evolutionary process. Method and theory in comparative biology. New York, Columbia University Press.

Eldredge N and Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In Schopf TJM (ed.) Models in paleobiology. San Francisco, Freeman: 82-115.

Eldredge N and Tattersall I (1975) Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. In Szalay FS (ed.) Approaches to primate paleobiology. Basel, Karger: 218-242.

Estabrook GF *et al.* (1977) An application of compatibility analysis to the Blackiths' data on Orthopteroid insects. Systematic Zoology 26: 269-276.

Falk D (1983) Cerebral cortices of East African early hominids. Science 221: 1072-1074.

Falk D (1986) Evolution of cranial blood drainage in hominids: enlarged occipital/marginal sinuses and emissary foramina. American Journal of Physical Anthropology 70: 311-324.

Falk D and Conroy GC (1983) The cranial venous sinus system in *Australopithecus afarensis*. Nature 306: 779-781.

Farris JS (1970) Methods for computing Wagner trees. Systematic Zoology 19: 83-92.

Feldesman MR (1979) Further morphometric studies of the ulna from the Omo basin, Ethiopia. American Journal of Physical Anthropology 51: 409-416.

Felsenstein J and Sober E (1980) Parsimony and likelihood: an exchange. Systematic Zoology 35: 617-626.

Fink WL (1986) Microcomputers and phylogenetic analysis. Science 234: 1135-1139.

Finnegan M and Rubison RM (1984) Multivariate distances and multivariate classification systems using non-metric traits in biological studies. In Van Vark GN and Howells WW (eds.) Multivariate statistical methods in physical anthropology. Dordrecht, Reidel: 69-80.

Fitch FJ and Miller JA (1970) Radioisotopic determinations of Lake Rudolf artefacts. Nature 226: 226-228.

Fitch WM (1971) Toward defining the course of evolution: minimum change for a specific tree topology. Systematic Zoology 20: 406-416.

Franzen JL (1985) What is "*Pithecanthropus dubius* Koenigswald, 1950"? In Delson E (ed.) Ancestors: the hard evidence. New York, Liss: 221- 226.

Frayer DW and Wolpoff MH (1985) Sexual dimorphism. Annual Review of Anthropology 14: 429-473.

Gause GF (1934) The struggle for existence. Baltimore: Williams and Wilkins.

Ghiselin MT (1974) A radical solution to the species problem. Systematic Zoology 23: 536-554.

Ghiselin MT (1976) The nomenclature of correspondence: a new look at "Homology" and "Analogy". In Masterton RB *et al.* (eds.)

Evolution, brain and behaviour: persistent problems. Hillsdale, Erlbaum: 129-142.

Gingerich PD (1977) Patterns of evolution in the mammalian fossil record. In Hallam A (ed.) Patterns of evolution. Amsterdam, Elsevier: 469-500.

Gingerich PD (1979) The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In Cracraft J and Eldredge N (eds.) Phylogenetic analysis and paleontology. New York, Columbia University Press: 41-77.

Gingerich PD and Schoeninger MJ (1979) Patterns of tooth size variability in the dentition of primates. American Journal of Physical Anthropology 51: 457-466.

Goodman M (1961) The role of immunochemical differences in the phyletic development of human behaviour. Human Biology 33: 131-162.

Goodman M (1986) Molecular evidence on the ape subfamily Homininae. Progress in Clinical and Biological Research 218: 121-132.

Gould SJ (1966) Allometry and size in ontogeny and phylogeny. Biological Reviews 41: 587-640.

Gould SJ (1977) Ontogeny and phylogeny. Harvard, Belknap.

Grine FE (1981) Trophic differences between 'gracile' and 'robust' australopithecines: a scanning electron microscope analysis of occlusal events. South African Journal of Science 77: 203-230.

Grine FE (1984) The deciduous dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene hominids. Ph.D. thesis, University of the Witwatersrand, Johannesburg.

Groves CP (1974) Taxonomy and phylogeny of prosimians. In Martin RD et al. (eds.) Prosimian biology. London, Duckworth: 449-473.

Groves CP (1986) Systematics of the great apes. In Swindler DR and Erwin J (eds.) Comparative primate biology. Volume 1: Systematics, evolution, and anatomy. New York, Liss: 187-217.

Groves GP and Mazak M (1975) An approach to the taxonomy of the Hominidae: gracile Villefranchian hominids of Africa. Casopis pro Mineralogii a Geologii 20: 225-247.

Guthrie WKC (1962) A history of Greek philosophy, Volume 1. Cambridge, Cambridge University Press.

Haeckel E (1899) Ueber unsere gegenwärtige Kenntnis vom Ursprung des Menschen. Bonn, Strauss.

Hall RL (ed.) (1982) Sexual dimorphism in Homo sapiens. New York, Praeger.

Hamilton WR (1978) Fossil giraffes from the Miocene of Africa and a revision of the Giraffoidea. Philosophical Transactions of the Royal Society of London (B) 283: 165-229.

Hardin G (1960) The competitive exclusion principle. Science 131: 1292-1297.

Harris JM (1983) Correlation of the Koobi Fora succession. In Harris JM (ed.) Koobi Fora Research Project, Volume 2. The fossil ungulates: Proboscidea, Perissodactyla, and Suidae. Oxford, Clarendon: 303-317.

Harris JM and White TD (1979) Evolution of the Plio Pleistocene African suidae. Transactions of the American Philosophical Society 69: 1-128.

Hasegawa M et al. (1984) A new molecular clock of mtDNA and the evolution of hominoids. Proceedings of the Japanese Academy of Science 60: 95-98.

Hay RL (1976) Geology of the Olduvai Gorge. A study of sedimentation in a semiarid basin. Berkeley, University of California Press.

Hennig W (1950) Grundzüge einer Theorie der phylogenetischen Systematik. Berlin, Deutscher Zentralverlag.

Hennig W (1965) Phylogenetic systematics. Annual Review of Entomology 10: 97-116.

Hills M (1978) On ratios - a response to Atchley, Gaskins, and Anderson. Systematic Zoology 27: 61-62.

Hills M et al. (1983) The allometry of relative cusp size in hominoid mandibular molars. American Journal of Physical Anthropology 62: 311-316.

Holloway RL (1965) Cranial capacity of the hominine from Olduvai, Bed I. Nature 208: 205-206.

Holloway RL (1966) Cranial capacity of the Olduvai Bed I Hominine. Nature 210: 1108-1109.

Holloway RL (1968) Current comment. Current Anthropology 9: 35-36.

Holloway RL (1970a) Australopithecine endocast (Taung specimen, 1924) a new volume determination. Science 168: 966-968.

Holloway RL (1970b) New endocranial volumes for the australopithecines. Nature 227: 199-200.

Holloway RL (1976) Some problems of hominid brain endocast reconstruction, allometry, and neural reorganisation. Prétirage, Premier Congrés International de Paléontologie Humain. Paris, CNRS: 69-119.

Holloway RL (1978) Problems of brain endocast interpretation and African hominid evolution. In Jolly CJ (ed.) Early Hominids of Africa. London, Duckworth: 379-401.

Holloway RL (1980) The OH 7 (Olduvai Gorge, Tanzania) hominid partial brain endocast revisited. American Journal of Physical Anthropology 53: 267-274.

Holloway RL (1983a) Human palaeontological evidence relevant to language behaviour. Human Neurobiology 2: 105-114.

Holloway RL (1983b) The OH 7 (Olduvai Gorge, Tanzania) parietal fragments and their reconstruction: a reply to Wolpoff. American Journal of Physical Anthropology 60: 505-516.

Holloway RL (1985) The past, present, and future significance of the lunate sulcus in early hominid evolution. In Tobias PV (ed.) Hominid evolution: Past, present and future. New York, Liss: 47-62.

Holloway RL and Post DG (1982) The relativity of relative brain measures and hominid mosaic evolution. In Armstrong E and Falk D (eds.) Primate brain evolution: methods and concepts. New York, Plenum: 57-76.

Hooijer DA and Kurtén B (1984) Trinil and Kedungbrubus: the Pithecanthropus-bearing fossil faunas of Java and their relative age. Annales Zoologici Fennici 21: 135-141.

Howell FC (1967) Recent advances in human evolutionary studies. Quarterly Review of Biology 42: 471-513.

Howell FC (1968) Omo research expedition. Nature 219: 567-572.

Howell FC (1969a) Hominid teeth from White Sands and Brown Sands localities, lower Omo basin (Ethiopia). Quaternaria 11: 47-64.

Howell FC (1969b) Remains of Hominidae from Pliocene/Pleistocene formations in the Lower Omo Basin, Ethiopia. Nature 223: 1234-1239.

Howell FC (1978) Hominidae. In Maglio VJ and Cooke HBS (eds.) Evolution of African mammals. Cambridge, Harvard University Press: 145-248.

Howells WW (1970) Mount Carmel man: morphological relationships. Proceedings, 8th International Congress of Anthropological and Ethnological Sciences, Tokyo and Kyoto, 1968. Volume 1, Anthropology: 269-272.

Howells WW (1973) Cranial variation in man: a study by multivariate analysis of patterns of difference among recent human populations. Peabody Museum Papers 67: 1-259.

Howells WW (1984) Introduction. In Van Vark GN and Howells WW (eds.) Multivariate statistical methods in physical anthropology. Dordrecht, Reidel: 1-11.

Hughes AR and Tobias PV (1977) A fossil skull probably of the genus Homo from Sterkfontein, Transvaal. Nature 265: 310-312.

Hunt K and Vitzthum VJ (1986) Dental metric assessment of the Omo fossils: implications for the phylogenetic position of Australopithecus africanus. American Journal of Physical Anthropology 71: 141-155.

Isaac GL (1984) The archaeology of human origins: studies of the Lower Pleistocene in East Africa 1971-1981. In Wendorf F and Close A (eds.) Advances in World Archaeology, Volume 3. London, Academic: 1-87.

Johanson DC (1986) Director's report. Institute of Human Origins Bulletin: 1-5.

Johanson DC and Taieb M (1976) Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. Nature 260: 293-297.

Johanson DC and White TD (1979) A systematic assessment of early African hominids. Science 202: 321-330.

Johanson DC et al. (1978a) A new species of the genus Australopithecus (Primates: Hominidae) from the Pliocene of Eastern Africa. Kirtlandia #28: 1-14.

Johanson DC et al. (1978b) Expedition internationale de l'Afar, Ethiopie (4e et 5e campagnes 1975-1977): nouvelles decouvertes d'Hominides et decouvertes d'industries lithiques pliocenes a Hadar. Comptes Rendus des séances de l' Académie des Sciences D 287: 237- 240.

Johanson DC et al. (1987) New partial skeleton of Homo habilis from Olduvai Gorge, Tanzania. Nature 327: 205-209.

Johnson DR et al. (1985) Measurement of biological shape: a general method applied to mouse vertebrae. Journal of Embryology and Experimental Morphology 90: 363-377.

Jones DL et al. (1986) Palaeomagnetic results from the Kromdraai and Sterkfontein sites. South African Journal of Science 82: 160-163.

Jungers WL (1982) Lucy's limbs: skeletal allometry and locomotion in Australopuithecus afarensis. Nature 297: 676-678.

Jungers WL and Grine FE (1986) Dental trends in the australopithecines: the allometry of mandibular molar dimensions. In Wood BA et al. (eds.) Major topics in primate and human evolution. Cambridge, Cambridge University Press: 203-219.

Kay RF (1982) Sivapithecus simonsi, a new species of Miocene hominoid, with comments on the phylogenetic status of the Ramapithecinae. International Journal of Primatology 3: 113-173.

Kay RF and Simons EL (1983) A reassessment of the relationship between later Miocene and subsequent Hominoidea. In Ciochon RL and Corruccini RS (eds.) New interpretations of ape and human ancestry. New York, Plenum: 577-624.

Kazmierczak J-B (1985) Analyse logarithmique. Deux exemples d'application. Revue Statistique Appliquée 33: 13-24.

Kennedy GE (1983) A morphometric and taxonomic assessment of a hominine femur from the lower member, Koobi Fora, Lake Turkana. American Journal of Physical Anthropology 61: 429-436.

Kennedy GE (1984) Are the Kow Swamp hominids "archaic"? American Journal of Physical Anthropology 65: 163-168.

Kimbel WH (1984) Variation in the pattern of cranial venous sinuses and hominid phylogeny. American Journal of Physical Anthropology 63: 243-263.

Kimbel WH et al. (1984) Cranial morphology of Australopithecus afarensis: a comparative study based on a composite reconstruction of the adult skull. American Journal of Physical Anthropology 64: 337-388.

Kluge AG and Farris JS (1969) Quantitative phyletics and the evolution of the anurans. Systematic Zoology 18: 1-32.

Koenigswald GHR von (1964) Early man in East Africa: new discoveries. Experientia 20: 1-3.

Krantz GS (1977) A revision of australopithecine body sizes. Evolutionary Theory 2: 65-94.

Latter BDH (1980) Genetic differences within and between populations of the major human subgroups. American Naturalist 116: 220-237.

Leakey LSB (1959) A new fossil skull from Olduvai. Nature 201: 967-970

Leakey LSB (1960) Recent discoveries at Olduvai Gorge. Nature 188: 1050-1052.

Leakey LSB (1961a) New finds at Olduvai Gorge. Nature 189: 649-650.

Leakey LSB (1961b) The juvenile mandible from Olduvai. Nature 191: 417-418.

Leakey LSB (1964) The evolution of man. Discovery 25(8): 48-49.

Leakey LSB (1966) Homo habilis, Homo erectus and the australopithecines. Nature 209: 1279-1281.

Leakey LSB and Leakey MD (1964) Recent discoveries of fossil hominids in Tanganyika: at Olduvai and near Lake Natron. Nature 202: 5-7.

Leakey LSB et al. (1964) A new species of the genus Homo from Olduvai Gorge. Nature 202: 7-9.

Leakey MD (1969) Recent discoveries of hominid remains at Olduvai Gorge, Tanzania. Nature 223: 754-756.

Leakey MD (1978) Olduvai fossil hominids: their stratigraphic positions and associations. In Jolly CJ (ed.) Early hominids of Africa. London, Duckworth: 3-16.

Leakey MD (1981) Tracks and tools. Philosophical Transactions of the Royal Society of London, B, 292: 95-102.

Leakey MD and Hay RL (1979) Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. Nature 278: 317-323.

Leakey MD and Hay RL (1982) The chronological position of the fossil hominids of Tanzania. Prétirage, Premier Congrés International de Paléontologie Humain. Paris, CNRS: 753-765.

Leakey MD et al. (1971) New hominid skull from Bed I, Olduvai Gorge, Tanzania. Nature 232: 308-312.

Leakey MD et al. (1976) Fossil hominids from the Laetoli Beds. Nature 262: 460-466.

Leakey REF (1970) New hominid remains and early artifacts from Northern Kenya. Nature 226: 223-224.

Leakey REF (1971) Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. Nature 231: 241-245.

Leakey REF (1972) Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1971. Nature 237: 264-269.

Leakey REF (1973a) Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1972. Nature 242: 170-173.

Leakey REF (1973b) Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. Nature 242: 447-450.

Leakey REF (1973c) Australopithecines and hominines: a summary of the evidence from the early Pleistocene of eastern Africa. Symposia of the Zoological Society of London #33: 53-69.

Leakey REF (1974) Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1973. Nature *248*: 653-656.

Leakey REF (1976a) New hominid fossils from the Koobi Fora formation in northern Kenya. Nature *261*: 574-576.

Leakey REF (1976b) Hominids in Africa. American Scientist *64*: 174-178.

Leakey REF (1976c) An overview of the hominidae from East Rudolf, Kenya. In Coppens Y *et al.* (eds.) Earliest man and environments in the Lake Rudolf Basin. Chicago, University of Chicago Press: 476-483.

Leakey REF and Walker AC (1976) *Australopithecus*, *Homo erectus* and the single species hypothesis. Nature *261*: 572-574.

Leakey REF and Walker AC (1985) Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. American Journal of Physical Anthropology *67*: 135-163.

Leakey REF and Wood BA (1973) New evidence of the genus *Homo* from East Rudolf, Kenya. II. American Journal of Physical Anthropology *39*: 355-368.

Leakey REF and Wood BA (1974) New evidence of the genus *Homo* from East Rudolf, Kenya (IV). American Journal of Physical Anthropology *41*: 237-244.

Leakey RE *et al.* (1978) The hominid catalogue. In MG Leakey and RE Leakey (eds.) Koobi Fora Research Project, Volume 1. The fossil hominids and an introduction to their context, 1968-1974. Oxford, Clarendon Press: 86-182.

Le Gros Clark WE (1964a) The evolution of man. Discovery *25*(7): 49.

Le Gros Clark WE (1964b) The fossil evidence for human evolution. Chicago, University of Chicago Press.

Le Quesne WJ (1969) A method of selection of characters in numerical taxonomy. Systematic Zoology *21*: 281-288.

Le Quesne WJ (1974) The uniquely evolved character concept and its cladistic application. Systematic Zoology *23*: 513-517.

Le Quesne WJ (1982) Compatibility analysis and its application. Zoological Journal of the Linnean Society *74*: 267-275.

Lestrel PE (1974) Some problems in the assessment of morphological size and shape differences. Yearbook of Physical Anthropology *18*: 140-162.

Lestrel PE and Roche A (1986) Cranial base shape variation with age: a longitudinal study of shape using Fourier analysis. Human Biology *58*: 527-540.

Lestrel PE et al. (1977) Size and shape of the hominoid distal femur: Fourier analysis. American Journal of Physical Anthropology 46: 281-290.

Lewis J et al. (1980) A nonhomogeneous anthropometric scaling method based on finite element principles. Journal of Biomechanics 13: 815-824.

Lewis OJ (1972) The evolution of the hallucial tarsometatarsal joint in the Anthropoidea. American Journal of Physical Anthropology 37: 13-26.

Lewis OJ (1973) The hominoid os capitatum, with special reference to the fossil bones from Sterkfontein and Olduvai Gorge. Journal of Human Evolution 2: 1-11.

Lewis OJ (1981) Functional morphology of the joints of the evolving foot. Symposia of the Zoological Society of London #46: 169-188.

Lewontin RC (1972) The apportionment of human diversity. Evolutionary Biology 6: 381-398.

Lieberman DE (1986) Homo habilis and the single species hypothesis: a proposal for a new species. BA Dissertation, Harvard College, Cambridge, Massachussets.

Lisowski FP (1967) Annular growth changes and comparisons in the primate talus. Folia Primatologica 7: 81-97.

Lisowski FP et al. (1974) The form of the talus in some higher primates: a multivariate study. American Journal of Physical Anthropology 41: 191-215.

Lisowski FP et al. (1976) African fossil tali: further multivariate morphometric studies. American Journal of Physical Anthropology 45: 5-18.

Lovejoy AO (1968) Buffon and the problem of species. In Glass B et al. (eds.) Forerunners of Darwin. Baltimore, John Hopkins Press: 84-113.

Lovejoy CO (1978) A biomechanical view of the locomotor diversity of early hominids. In Jolly CJ (ed.) Early hominids of Africa. London, Duckworth: 403-429.

Lovejoy CO (1981) The origin of man. Science 211: 341-350.

Maddison WP et al. (1984) Outgroup analysis and parsimony. Systematic Zoology 33: 83-103.

Mann A (1970) "Telanthropus" and the single species hypothesis: a further comment. American Anthropologist 72: 607-609.

Martin LB (1983) The relationships of the later Miocene hominoidea. Ph.D. thesis, University of London.

Martin L (1985) Significance of enamel thickness in hominoid evolution. Nature 314: 260-263.

Martin L (1986) Relationships among extant and extinct great apes and humans. In Wood BA et al. (eds.) Major topics in primate and human evolution. Cambridge, Cambridge University Press: 161-187.

Martin R (1928) Lehrbuch der Anthropologie in systematischer Darstellung. 2nd Edition. Jena, Fischer.

Matsu'ura S (1982) A chronological framing for the Sangiran hominids. Fundamental study by the fluorine dating method. Bulletin of the National Science Museum, Tokyo (D) 8: 1-53.

Mayr E (1950) Taxonomic categories in fossil hominids. Cold Spring Harbor Symposia in Quantitative Biology 15: 109-118.

Mayr E (1963) Animal species and evolution. Cambridge, Belknap.

Mayr E (1965) Numerical phenetics and taxonomic theory. Systematic Zoology 14: 73-97.

Mayr E (1969) Principles of systematic zoology. New York, McGraw Hill.

Mayr E (1974) Cladistic analysis or cladistic classification. Zeitschrift für Zoologische Systematik und Evolutionsforschung 12: 94-128.

McDougall I (1985) K-Ar and $^{40}Ar/^{39}Ar$ dating of the hominid-bearing Pliocene-Pleistocene sequence at Koobi Fora, Lake Turkana, northern Kenya. Geological Society of America Bulletin 96: 159-175.

McHenry HM (1973) Early hominid humerus from East Rudolf, Kenya. Science 180: 739-741.

McHenry HM (1975a) A new pelvic fragment from Swartkrans and the relationship between the robust and gracile australopithecines. American Journal of Physical Anthropology 43: 245-262.

McHenry HM (1975b) Fossil hominid body weight and brain size. Nature 254: 686-688.

McHenry HM (1983) The capitate of Australopithecus afarensis and A. africanus. American Journal of Physical Anthropology 62: 187-198.

McHenry HM (1984) Relative cheek-tooth size in Australopithecus. American Journal of Physical Anthropology 64: 297-306.

McHenry HM (1986) Size variation in the postcranium of Australopithecus afarensis and extant species of

Hominoidea. Human Evolution 1: 149-156.

McHenry HM and Corruccini RS (1975a) Multivariate analysis of early hominid pelvic bones. American Journal of Physical Anthropology 43: 263-270.

McHenry HM and Corruccini RS (1975b) Distal humerus in hominoid evolution. Folia Primatologica 23: 227-244.

McHenry HM and Corruccini RS (1976) Fossil hominid femora. Nature 264: 813.

McHenry HM and Corruccini RS (1978) Analysis of the hominoid os coxae by Cartesian coordinates. American Journal of Physical Anthropology 48: 215-226.

McHenry HM et al. (1976) Analysis of an early hominid ulna from the Omo basin, Ethiopia. American Journal of Physical Anthropology 44: 295-304.

Miyamoto MM and Goodman M (1986) Biomolecular systematics of eutherian mammals: phylogenetic patterns and classification. Systematic Zoology 35: 230-240.

Montagu A (1965) Homo habilis. Science 149: 918.

Mosimann JE (1970) Size allometry: size and shape variables with characterisations of the lognormal and generalised gamma distributions. Journal of the American Statistical Association 65: 930-945.

Napier JR (1962) Fossil hand bones from Olduvai Gorge. Nature 196: 409-411.

Nelson G (1978) Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology 27: 324-345.

Oakley KP (1964) The evolution of man. Discovery 25(8): 49.

Oakley KP and Campbell BG (1964) Newly described Olduvai hominid. Nature 202: 732.

Olshan AF et al. (1982) Robust and least-squares orthogonal mapping: methods for the study of cephalofacial form and growth. American Journal of Physical Anthropology 59: 131-138.

Olson TR (1978) Hominid phylogenetics and the existence of Homo in Member 1 of the Swartkrans Formation, South Africa. Journal of Human Evolution 7: 159-178.

Olson TR (1981) Basicranial morphology of the extant hominoids and Pliocene hominids: the new material from the Hadar Formation, Ethiopia and its significance in early human evolution and taxonomy. In Stringer CB (ed.) Aspects of human evolution. London, Taylor and Francis: 99-128.

Olson TR (1985) Cranial morphology and sysytematics of the Hadar Formation hominids and "Australopithecus" africanus. In Delson E (ed.) Ancestors, the hard evidence. New York, Liss: 102-119.

Oxnard CE (1969) A note on the Olduvai clavicular fragment. American Journal of Physical Anthropology 29: 429-432.

Oxnard CE (1972) Some African fossil foot bones: a note on the interpolation of fossils into a matrix of extant species. American Journal of Physical Anthropology 37: 3-12.

Oxnard CE (1973) Functional inferences from morphometrics: problems posed by uniqueness and diversity among the primates. Systematic Zoology 22: 409-424.

Oxnard CE (1975) The place of the australopithecines in human evolution: grounds for doubt? Nature 258: 389-395.

Oxnard CE (1984) The order of man. New Haven, Yale University Press.

Paterson HEH (1978) More evidence against speciation by reinforcement. South African Journal of Science 74: 369-371.

Paterson HE (1980) A comment on "mate recognition systems". Evolution 34: 330-331.

Paterson HEH (1981) The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. South African Journal of Science 77: 113-119.

Paterson HEH (1982) Perspective on speciation by reinforcement. South African Journal of Science 78: 53-57.

Paterson HEH (1985) The recognition concept of species. In Vrba ES (ed.) Species and speciation. Transvaal Museum Monograph #4. Pretoria, Transvaal Museum: 21-29.

Patterson B and Howells WW (1967) Hominid humeral fragment from early Pleistocene of Northwestern Kenya. Science 156: 64-66.

Patterson C (1982) Morphological characters and homology. In Joysey KA and Friday AE (eds.) Problems of phylogenetic reconstruction. Systematics Association Special Volume #21. London, Academic Press: 21-74.

Penny D (1982) Graph theory, evolutionary trees and classification. Zoological Journal of the Linnean Society 74: 277-292.

Penrose LS (1954) Distance, size and shape. Annals of Eugenics 18: 337-343.

Pilbeam DR (1969) Early Hominidae and cranial capacity. Nature 224: 386.

Pilbeam DR (1970) Early Hominidae and cranial capacities. Nature 227: 747-748.

Pilbeam DR and Gould SJ (1974) Size and scaling in human evolution. Science 186: 892-901.

Pilbeam DR and Simons EL (1965) Some problems of hominid classification. American Scientist 53: 237-259.

Preuschoft H (1971) Body posture and mode of locomotion in early Pleistocene hominids. Folia Primatologica 14: 209-240.

Rak Y (1983) The australopithecine face. New York, Academic Press.

Rak (1985) Australopithecine taxonomy and phylogeny in light of facial morphology. American Journal of Physical Anthropology 66: 281-287.

Raup DM (1972) Approaches to morphological analysis. In Schopf TJM (ed.) Models in paleobiology. San Francisco, Freeman: 28-44.

Read DW (1975) Hominid teeth and their relationship to hominid phylogeny. American Journal of Physical Anthropology 42: 105-126.

Read DW (1984) From multivariate statistics to natural selection: a reanalysis of the Plio/Pleistocene hominid dental material. In Van Vark GN and Howells WW (eds.) Statistical methods in physical anthropology. Dordrecht, Reidel: 377-413.

Reed CA (1967) The generic allocation of the hominid species habilis as a problem in systematics. South African Journal of Science 63: 3-5.

Reist JD (1985) An empirical investigation of several univariate methods that adjust for size variation in morphometric data. Canadian Journal of Zoology 63: 1429-1439.

Richard AF (1985) Primates in nature. New York, Freeman.

Rieppel O (1986) Species are individuals: review and critique of the argument. Evolutionary Biology 20: 283-317.

Rightmire GP (1969) On the computation of Mahalanobis' Generalised Distance (D^2). American Journal of Physical Anthropology 30: 157-160.

Rightmire GP (1972) Multivariate analysis of an early hominid metacarpal from Swartkrans. Science 176: 159-161.

Rightmire GP (1980) Middle Pleistocene hominids from Olduvai Gorge, Northern Tanzania. American Journal of Physical Anthropology 53: 225-241.

Rightmire GP (1981) Patterns in the evolution of Homo erectus. Paleobiology 7: 241-246.

Rightmire GP (1984) Comparisons of Homo erectus from Africa and Southeast Asia. Courier Forschungsinstitut Senckenberg #69: 83-98.

Rightmire GP (1986) Stasis in Homo erectus defended. Paleobiology 12: 324-325.

Robinson JT (1953) Telanthropus and its phylogenetic significance. American Journal of Physical Anthropology 11: 445-501.

Robinson JT (1954) The genera and species of the Australopithecinae. American Journal of Physical Anthropology 12: 181-200.

Robinson JT (1965) Homo 'habilis' and the australopithecines. Nature 205: 121-124.

Robinson JT (1966) The distinctiveness of Homo habilis. Nature 209: 957-960.

Robinson JT (1967) Variation and the taxonomy of the early hominids. Evolutionary Biology 1: 69-100.

Robinson JT (1970) Two new early hominid vertebrae from Swartkrans. Nature 225: 1217-1219.

Robinson JT (1972a) The bearing of East Rudolf fossils on early hominid systematics. Nature 240: 239-240.

Robinson JT (1972b) Early hominid posture and locomotion. Chicago, University of Chicago Press.

Robinson JT and Steudel K (1973) Multivariate discriminant analysis of dental data bearing on early hominid affinities. Journal of Human Evolution 2: 509-527.

Rose MD (1984) A hominine hip bone, KNM-ER 3228, from East Turkana, Kenya. American Journal of Physical Anthropology 63: 371-378.

Roth VL (1984) On homology. Biological Journal of the Linnean Society 22: 13-29.

Ryan MJ (1986) Neuroanatomy influences speciation rate among mammals. Proceedings of the National Academy of Science 83: 1379-1382.

Saban R (1980) Le trace des veines meningees moyennes sur le moulage endocranien d'Homo habilis (KNM-ER 1470). Comptes Rendus des séances de l' Académie des Sciences D 290: 405-408.

Saban R (1982) Les empreintes endocraniennes des veins meningees moyennes et les etapes de l'evolution humaine. Annales de Paléontologie 68: 171-220.

Savatier P et al. (1987) Nucleotide sequence of the beta-globin genes in Gorilla and Macaque: the origin of nucleotide polymorphisms in human. Journal of Molecular Evolution 24: 309-318.

Schmitt TJ and Nairn AEM (1984) Interpretations of the magnetostratigraphy of the Hadar hominid site, Ethiopia. Nature 309: 704-706.

Schwalbe G (1906) Studien zur Vorgeschichte des Menschen. Stuttgart, Schweizerbartsche.

Schwartz JH et al. (1978) Phylogeny and classification of the primates revisited. Yearbook of Physical Anthropology 21: 95-133.

Seilacher A (1970) Arbeitskonzept zur Konstruktions-Morphologie. Lethaia 3: 393-396.

Sibley CG and Ahlquist JE (1984) The phylogeny of the hominoid primates as indicated by DNA:DNA hybridisation. Journal of Molecular Evolution 20: 2-15.

Siegel AF et al. (1982) A robust comparison of biological shapes. Biometrics 38: 341-350.

Simons EL (1972) Primate evolution. An introduction to man's place in nature. New York, Macmillan.

Simpson GG (1951) The species concept. Evolution 5: 285-298.

Simpson GG (1961) Principles of animal taxonomy. New York, Columbia University Press.

Simpson GG et al. (1960) Quantitative zoology. Revised edition. New York, Harcourt, Brace and World.

Skalak R et al. (1982) Analytical description of growth. Journal of Theoretical Biology 94: 555-577.

Skelton RR et al. (1986) Phylogenetic analysis of early hominids. Current Anthropology 27: 21-43.

Smith RJ (1981) Interpretation of corre3lations in intraspecific and interspeciic allometry. Growth 45: 291-297.

Sneath PHA (1967) Trend-surface analysis of transformation grids. Journal of the Zoological Society of London 151: 65-122.

Sokal RR and Rohlf FJ (1981) Biometry. The principles and practice of statistics in biological research. San Francisco, Freeman.

Sokal RR and Sneath PHA (1963) Principles of numerical taxonomy. San Francisco, Freeman.

Somers KM (1986) Multivariate allometry and removal of size with principal components analysis. Systematic Zoology 35: 359-368.

Sondaar PY (1984) Faunal evolution and the mammalian biostratigraphy of Java. Courier Forschungsinstitut Senckenberg #69: 219-235.

SPSS Inc. (1986) SPSSX User's guide. 2nd Edition. New York, McGraw Hill.

Stern JT and Susman RL (1983) The locomotor anatomy of Australopithecus afarensis. American Journal of Physical Anthropology 60: 279-317.

Steudel K (1978) A multivariate analysis of early hominids. Journal of Human Evolution 7: 583-595.

Stevens PF (1980) Evolutionary polarity of character states. Annual Review of Ecology and Systematics 11: 333-358.

Stringer CB (1974) Population relationships of later Pleistocene hominids: a multivariate study of available crania. Journal of Archaeological Science 1: 317-342.

Stringer CB (1981) The dating of European Middle Pleistocene hominids and the existence of Homo erectus in Europe. Anthropologie 19: 3-14.

Stringer CB (1984) Human evolution and biological adaptation in the Pleistocene. In Foley R (ed.) Hominid evolution and community ecology. London, Academic Press: 55-83.

Stringer CB (1986) The credibility of Homo habilis. In Wood BA et al. (eds.) Major topics in primate and human evolution. Cambridge, Cambridge Univerity Press: 266-294.

Stringer CB et al. (1985) Preparation and further study of the Singa skull from Sudan. Bulletin of the British Museum of Natural History (Geology) 38: 347-358.

Susman RL and Creel N (1979) Functional and morphological affinities of the subadult hand (OH 7) from Olduvai Gorge. American Journal of Physical Anthropology 51: 311-332.

Susman RL and Stern JT (1979) Telemetred myography of flexor digitorum profundus and flexor digitorum superficialis in Pan troglodytes and implications for interpretation of the O.H. 7 hand. American Journal of Physical Anthropology 50: 565-574.

Susman RL and Stern JT (1982) Functional morphology of Homo habilis. Science 217: 931-934.

Susman RL et al. (1984) Arboreality and bipedality in the Hadar hominids. Folia Primatologica 43: 113-156.

Sweet SS (1980) Allometric influence in morphology. American Zoologist 20: 643-652.

Swofford DR (1985) PAUP. Phylogenetic analysis using parsimony. Version 2.4. Champaign, Illinois Natural History Survey.

Taieb M et al. (1974) Decouverte d'Hominides dans les series plio-pleistocenes d'Hadar (Bassin de l'Awash; Afar, Ethiopie). Comptes Rendus des séances de l' Académie des Sciences D 279: 735-738.

Taieb M et al. (1975) Expedition internationale de l'Afar, Ethiopie (3eme campagne 1974), decouverte d'Hominides plio-pleistocenes a Hadar. Comptes Rendus des séances de l' Académie des Sciences D 281: 1297-1300.

Tardieu C (1981) Morpho-functional analysis of the articular surfaces of the knee-joint in primates. In Chiarelli AB and Corruccini RS (eds.) Primate evolutionary biology. Berlin, Springer: 68-80.

Tattersall I (1986) Species recognition in human paleontology. Journal of Human Evolution 15: 167-175.

Tattersall I and Eldredge N (1977) Fact, theory, and fantasy in human paleontology. American Scientist 65: 204-211.

Thorne AG and Wolpoff MH (1981) Regional continuity in Australasian Pleistocene hominid evolution. American Journal of Physical Anthropology 55: 337-349.

Tobias PV (1964a) The Olduvai Bed I hominine with special regard to its cranial capacity. Nature 202: 3-4.

Tobias PV (1964b) Letter to the editor. Discovery 25(8): 49-50.

Tobias (1965a) Cranial capacity of the hominine from Olduvai, Bed I. Nature 208: 206.

Tobias PV (1965b) Early man in East Africa. Science 149: 22-33.

Tobias (1965c) New discoveries in Tanganyika: their bearing on hominid evolution. Current Anthropology 6: 391-399 and 406-411.

Tobias PV (1966a) The distinctiveness of Homo habilis. Nature 209: 953-957.

Tobias PV (1966b) Cranial capacity of the Olduvai Bed I hominine. Nature 210: 1109-1110.

Tobias (1966c) Fossil hominid remains from Ubeidiyah, Israel. Nature 211: 130-133.

Tobias PV (1967) Olduvai Gorge, Volume 2. The cranium and maxillary dentition of *Australopithecus* (*Zinjanthropus*) *boisei*. Cambridge, Cambridge University Press.

Tobias PV (1968) The taxonomy and phylogeny of the australopithecines. In Chiarelli B (ed.) Taxonomy and phylogeny of old world primates with reference to the origin of man. Turin, Rosenberg and Seller: 277-315.

Tobias PV (1972) "Dished faces", brain size and early hominids. Nature *239*: 468-469.

Tobias PV (1973a) Implications of the new age estimates of the early South African hominids. Nature *246*: 79-83.

Tobias PV (1973b) New developments in hominid paleontology in south and east Africa. Annual Review of Anthropology *2*: 311-334.

Tobias PV (1973c) Darwin's prediction and the African emergence of the genus *Homo*. Accademia Nazionale dei Cincei, Quaderno #*182*: 63-85.

Tobias PV (1978a) Position et role des Australopithecines dans la phylogenese humaine, avec etude particuliere de *Homo habilis* et des theories controversees avancees a propos des premiers hominides fossiles de Hadar et de Laetolil. In Les origines humaines et les epoques de l'intelligence. Paris, Masson: 38-77.

Tobias PV (1978b) The earliest Transvaal members of the genus *Homo* with another look at some problems of hominid taxonomy and systematics. Zeitschrift für Morphologie und Anthropologie *69*: 225-265.

Tobias PV (1980a) The natural history of the helicoidal occlusal plane and its evolution in early *Homo*. American Journal of Physical Anthropology *53*: 173-187.

Tobias PV (1980b) A survey and synthesis of the African hominids of the late Tertiary and early Quaternary periods. In Königsson LK (ed.) Current argument on early man. Oxford, Pergamon: 86-113.

Tobias PV (1980c) "Australopithecus afarensis" and *A. africanus*: critique and an alternative hypothesis. Palaeontologia Africana *23*: 1-17.

Tobias PV (in preparation) Olduvai Gorge, Volume 4. Cambridge, Cambridge University Press.

Tobias PV and Koenigswald GHR von (1964) Comparison between the Olduvai hominines and those of Java and some implications for hominid phylogeny. Nature *204*: 515-518.

Tooby J and DeVore I (1987) The reconstruction of hominid behavioural evolution through strategic modelling. In Kinzey WG (ed.) The evolution of human behaviour: primate models. Albany, SUNY Press: 183-237.

Trinkaus E (1984) Does KNM-ER 1481A establish Homo erectus at 2.0 Myr BP? American Journal of Physical Anthropology 64: 137-139.

Turner A (1985) The recognition concept of species in palaeontology, with special consideration of some issues in hominid evolution. In Vrba ES (ed.) Species and speciation. Transvaal Museum Monograph #4. Pretoria, Transvaal Museum: 153-158.

Turner A (1986) Species, speciation and human evolution. Human Evolution 1: 419-430.

Tuttle RH (1967) Knuckle-walking and the evolution of hominid hands. American Journal of Physical Anthropology 26: 171-206.

Vaisnys JR et al. (1984) An alternative method of estimating the cranial capacity of Olduvai Hominid 7. American Journal of Physical Anthropology 65: 71-81.

Van Valen L (1976) Ecological species, multispecies, and oaks. Taxon 25: 233-239.

Van Valen LM (1982) Homology and its causes. Journal of Morphology 173: 305-312.

Van Vark GN (1970) Some statistical procedures for the investigation of prehistoric human skeletal material. Ph.D. thesis, University of Groningen.

Van Vark GN (1984) On the determination of hominid affinities. In Van Vark GN and Howells WW (eds.) Multivariate statistical methods in anthropology. Dordrecht, Reidel: 323-349.

Vrba ES (1979a) Phylogenetic analysis and classification of fossil and recent Alcelaphini (Family Bovidae, Mammalia). Zoological Journal of the Linnean Society 11: 207-228.

Vrba ES (1979b) A new study of the scapula of Australopithecus africanus from Sterkfontein. American Journal of Physical Anthropology 51: 117-130.

Vrba ES (1980) Evolution, species and fossils: how does life evolve? South African Journal of Science 76: 61-84.

Vrba ES (1981) The Kromdraai australopithecine site revisited in 1980; recent investigation and results. Annals of the Transvaal Musem 33: 17-60.

Vrba ES (1982) Biostratigraphy and chronology, based particularly on Bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and

Cave of Hearths. Prétirage, Premier Congrés International de Paléontologie Humain. Paris, CNRS: 707-752.

Vrba ES (1984) Evolutionary pattern and process in the sister group Alcelaphini-Aepycerotini (Mammalia: Bovidae). In Eldredge N and Stanley SM (eds) Living fossils. New York, Springer: 62-79.

Walker A (1976) Remains attributable to Australopithecus in the East Rudolf succession. In Coppens Y et al. (eds.) Earliest man and environments in the Lake Rudolf Basin. Chicago, University of Chicago Press: 484-489.

Walker A and Leakey R (1978) The hominids of East Turkana. Scientific American 239(2): 44-56.

Walker A et al. (1986) 2.5-Myr Australopithecus boisei from west of Lake Turkana, Kenya. Nature322: 517-522.

Wallace J (1975) Dietary adaptations of Australopithecus and early Homo. In Tuttle RH (ed.) Paleoanthropology: morphology and paleoecology. The Hague, Mouton: 203-223.

Wallace JA (1977) Gingival eruption sequences of permanent teeth in early hominids. American Journal of Physical Anthropology 46: 483-494.

Wallace J (1978) Evolutionary trends in the early hominid dentition: a study in palaeoanatomy. In Jolly CJ (ed.) Early hominids of Africa. London, Duckworth: 285-310.

Ward SC and Pilbeam DR (1983) Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan. In Ciochon RL and Corruccini RS (eds.) New interpretations in ape and human ancestry. New York, Plenum: 211-238.

Weidenreich F (1943) The skull of Sinanthropus pekinensis; a comparative study on a primitive hominid skull. Palaeontologia Sinica New Series D, No. 10: 1-486.

Weidenreich F (1945) Giant early-man from Java and South China. Anthropological Papers of the American Museum of Natural History 40: 1-134.

Wells LH (1973) Forward from Taung. Journal of Human Evolution 2: 563-566.

White L (1959) The evolution of culture. New York, McGraw Hill.

White TD (1977) The anterior mandibular corpus of early African Hominidae: functional significance of shape and size. Ph.D. thesis, University of Michigan.

White TD (1980) Additional fossil hominids from Laetoli, Tanzania: 1976-1979 specimens. American Journal of Physical Anthropology 53: 487-504.

White TD (1985) The hominids of Hadar and Laetoli: an element-by-element comparison of the dental samples. In Delson E (ed.) Ancestors: the hard evidence. New York, Liss: 138-152.

White TD and Harris JM (1977) Suid evolution and correlation of African hominid localities. Science 198: 13-21.

White TD et al. (1981) Australopithecus africanus: its phyletic position reconsidered. South African Journal of Science 77: 445-470.

Wiley EO (1978) The evolutionary species concept reconsidered. Systematic Zoology 27: 17-26.

Wolpoff MH (1968) "Telanthropus" and the single species hypothesis. American Anthropologist 70: 477-493.

Wolpoff MH (1969) Cranial capacity and taxonomy of Olduvai Hominid 7. Nature 23: 182-183.

Wolpoff MH (1970) The evidence for multiple taxa at Swartkrans. American Anthropologist 72: 576-607.

Wolpoff MH (1971a) Is the new composite cranium from Swartkrans a small robust australopithecine? Nature 230: 398-401.

Wolpoff MH (1971b) Competitive exclusion among Lower Pleistocene hominids: the single species hypothesis. Man 6: 601-614.

Wolpoff MH (1976) Some aspects of the evolution of early hominid sexual dimorphism. Current Anthropology 17: 113-139.

Wolpoff MH (1977) Systematic variation in early hominid corpus dimensions. Anthropologia Anzeiger 36: 3-6.

Wolpoff MH (1978) Some aspects of canine size in the australopithecines. Journal of Human Evolution 7: 115-126.

Wolpoff MH (1981) Cranial capacity estmates for Olduvai Hominid 7. American Journal of Physical Anthropology 56: 297-304.

Wolpoff MH (1982) Relative canine size. Journal of Human Evolution 10: 151-158.

Wolpoff MH (1983) Lucy's little legs. Journal of Human Evolution 12: 443-453.

Wolpoff MH (1984) Evolution in Homo erectus: the question of stasis. Paleobiology 10: 389-406.

Wood BA (1974) Olduvai Bed I post-cranial fossils: a reassessment. Journal of Human Evolution 3: 373-378.

Wood BA (1976a) Remains attributable to Homo in the East Rudolf succession. In Coppens Y *et al.* (eds.) Earliest man and environments in the Lake Rudolf Basin. Chicago, University of Chicage Press: 490-506.

Wood BA (1976b) The nature and basis of sexual dimorphism in the primate skeleton. Journal of Zoology 180: 15-34.

Wood BA (1978a) Classification and phylogeny of East African hominids. In Chivers DJ and Joysey KA (eds.) Recent Advances in Primatology, Volume 3: Evolution. New York, Academic: 351-372.

Wood BA (1978b) Allometry and hominid studies. In Bishop WW (ed.) Geological background to fossil man. Edinburgh, Scottish Academic Press: 125-138.

Wood BA (1979) Models for assessing relative canine size in fossil hominids. Journal of Human Evolution 8: 493-502.

Wood BA (1984) The origin of *Homo erectus*. Courier Forschungsinstitut Senckenberg #69: 99-111.

Wood BA (1985a) Early *Homo* in Kenya, and its systematic relationships. In Delson E (ed.) Ancestors: the hard evidence. New York, Liss: 206-214.

Wood BA (1985b) Sexual dimorphism in the hominid fossil record. In Ghesquiere J *et al.* (eds.) Human sexual dimorphism. London, Taylor and Francis: 105-123.

Wood BA (in preparation) Cranial remains from Koobi Fora, Kenya. Oxford, Clarendon Press.

Wood BA and Abbott SA (1983) Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. Journal of Anatomy 136: 197-219.

Wood BA and Chamberlain AT (1986) *Australopithecus*: grade or clade? In Wood BA *et al.* (eds.) Major topics in primate and human evolution. Cambridge, Cambridge University Press: 220-248.

Wood BA and Chamberlain AT (in press) The nature and affinities of the 'robust' australopithecines. Journal of Human Evolution.

Wood BA and Stack CG (1980) Does allometry explain the difference between 'gracile' and 'robust australopithecines? American Journal of Physical Anthropology 52: 55-62.

Wood BA and Van Noten FL (1986) Preliminary observations on the BK8518 mandible from Baringo, Kenya. American Journal of Physical Anthropology 69: 117-127.

Wood BA *et al.* (1983) Analysis of the dental morphology of

Plio-Pleistocene hominids. II. Mandibular molars - study of cusp areas, fissure patterns and cross-sectional shape of the crown. Journal of Anatomy 137: 287-314.

Wood BA et al. (in press) Analysis of the dental morphology of Plio-Pleistocene hominids. 4. Mandibular premolar root morphology. Journal of Anatomy.

Wood DS (1983) Character transformations in phenetic studies using continuous morphometric variables. Systematic Zoology 32: 125-131.

Wu R-K and Oxnard CE (1983) Ramapithecines from China: evidence from tooth dimensions. Nature 306: 258-260.

Yasui K (1986) Method for analysing outlines with an application to recent Japanese crania. American Journal of Physical Anthropology 71: 39-49.

Zuckerman S et al. (1973) Some locomotor features of the pelvic girdle in primates. Symposia of the Zoological Society of London #33: 71-165.

APPENDIX 1

Catalogue numbers and locations of primate and modern human specimens used in this study

Colobus guereza

Catalogue No.	Sex	Location
3013	F	KNM-N
3015	F	KNM-N
3042	F	KNM-N
3044	F	KNM-N
3045	F	KNM-N
3061	F	KNM-N
3066	F	KNM-N
3069	F	KNM-N
3077	F	KNM-N
3094	F	KNM-N
355	M	KNM-N
3052	M	KNM-N
3055	M	KNM-N
3059	M	KNM-N
3063	M	KNM-N
3067	M	KNM-N
3071	M	KNM-N
3078	M	KNM-N
3081	M	KNM-N
3084	M	KNM-N

Papio anubis

Catalogue No.	Sex	Location
426	F	KNM-N
442	F	KNM-N
445	F	KNM-N
465	F	KNM-N
3143	F	KNM-N
3144	F	KNM-N
3150	F	KNM-N
3153	F	KNM-N
3157	F	KNM-N
3158	F	KNM-N
3145	M	KNM-N
3151	M	KNM-N
3152	M	KNM-N
3159	M	KNM-N
3161	M	KNM-N
3163	M	KNM-N
6429	M	KNM-N
6614	M	KNM-N
6616	M	KNM-N
6618	M	KNM-N

Hylobates lar

10.10.1.7	F	BMN-L
10.10.1.8	F	BNM-L
14.12.8.7	F	BMN-L
14.12.8.8	F	BMN-L
24.9.2.6	F	BMN-L
24.9.2.7	F	BMN-L
55.1493	F	BMN-L
55.1498	F	BMN-L
55.1500	F	BMN-L
1914.8.22.1	F	BMN-L
14.12.8.1	M	BMN-L
14.12.8.2	M	BMN-L
14.12.8.3	M	BMN-L
14.12.8.5	M	BMN-L
14.12.8.6	M	BMN-L
14.8.22.2	M	BMN-L
24.9.2.2	M	BMN-L
24.9.2.3	M	BMN-L
55.1494	M	BMN-L
55.1497	M	BMN-L

Pongo pygmaeus

3.00	F	BMN-L
3.mm	F	BMN-L
1179.c	F	BMN-L
1948.7.6.1	F	BMN-L
1976.1427	F	BMN-L
1976.1430	F	BMN-L
3.a	F	NMG-L
1963.173.12	F	NMG-L
LA.2.86	F	ULA-L
LA.4.86	F	ULA-L
3.e.e	M	BMN-L
56.11.8.2	M	BMN-L
1868.4.16.2	M	BMN-L
1979.1019	M	BMN-L
1948.10.30.1	M	BMN-L
1963.173.13	M	NMG-L
1984.54.11	M	NMG-L
LA.1.86	M	ULA-L
LA.11.86	M	ULA-L
LA.19.86	M	ULA-L

APPENDIX 1 [Contd.]

Gorilla gorilla

Catalogue No.	Sex	Location
F.C.146	F	PCM-B
M.460	F	PCM-B
M.729	F	PCM-B
M.878	F	PCM-B
Z.II.63	F	PCM-B
2.7.79.1	F	NMG-L
4.12.31	F	NMG-L
1979.420	F	NMG-L
1979.422	F	NMG-L
LA.20.86	F	ULA-L
F.C 115	M	PCM-B
F.C.133	M	PCM-B
M.342	M	PCM-B
M.505	M	PCM-B
M.717	M	PCM-B
1965.173.15	M	NMG-L
1984.54.2	M	NMG-L
1984.54.3	M	NMG-L
48.435	M	BMN-L
48.436	M	BMN-L

Pan troglodytes

Catalogue No.	Sex	Location
20.4.13.2	F	BMN-L
64.12.1.7	F	BMN-L
1939.992	F	BMN-L
1939.3369	F	BMN-L
1939.3378	F	BMN-L
1939.3382	F	LUA-L
LA.6.86	F	LUA-N
LA.8.86	F	LUA-L
TW.13.84	F	LUA-L
1982.546	F	NMG-L
1.8.9.10	M	BMN-L
2.a	M	BMN-L
24.8.6.1	M	BMN-L
50.1863	M	BMN-L
76.1797	M	BMN-L
1922.12.19.1	M	BMN-L
1939.951	M	BMN-L
1939.3363	M	BMN-L
1939.3364	M	BMN-L
1939.3365	M	BMN-L

Homo sapiens

A.2213	F	UWA-J
A.2307	F	UWA-J
A.2764	F	UWA-J
A.2848	F	UWA-J
A.2849	F	UWA-J
A.2890	F	UWA-J
A.3059	F	UWA-J
A.3124	F	UWA-J
A.3272	F	UWA-J
A.3291	F	UWA-J
A.2921	M	UWA-J
A.2966	M	UWA-J
A.3028	M	UWA-J
A.3072	M	UWA-J
A.3115	M	UWA-J
A.3277	M	UWA-J
A.3279	M	UWA-J
A.3286	M	UWA-J
A.3287	M	UWA-J
A.3315	M	UWA-J

KEY TO LOCATIONS OF SPECIMENS

BMN-L	British Museum (Natural History), London, U.K.
KNM-N	National Museums of Kenya, Nairobi, Kenya.
NMG-L	National Museums and Galleries on Merseyside (Liverpool Museum), Liverpool, U.K.
PCM-B	Powell-Cotton Museum, Birchington, Kent, U.K.
ULA-L	Department of Human Anatomy and Cell Biology, University of Liverpool, Liverpool, U.K.
UWA-J	Department of Anatomy, University of the Witwatersrand, Johannesburg, South Africa.

APPENDIX 2

Definitions of craniometric points and planes

AL (alveolare)	The most inferior point on the alveolar septum between the upper central incisors.
AS (asterion)	The common meeting point of the temporal, parietal and occipital bones.
BF	The most inferior point on the mandible below the centre of the mental foramen.
BM$_1$ & BM$_3$	The most inferior points on the mandibular corpus below the centres of the crowns of M$_1$ & M$_3$.
BP	The point on the inferior border of the parietal that is most distant from a corresponding point on the opposite side of the cranium in the same coronal plane (these points exclude the temporal-nuchal crest).
BR (bregma)	The posterior border of the frontal bone, in the median plane. If accessory bones are present this point is located on the general course of the coronal suture.
BS (basion)	The inferior edge of the anterior border of the foramen magnum, in the midline.

C'B, C'L etc.	The centre of the alveolar margin on the buccal (lingual etc.) side of C'.
C.P.	The plane perpendicular to F.H. and S.P., passing through left porion.
CS	The point in the median plane on the external surface of the mandibular symphysis, at the position where the breadth perpendicular to the symphyseal long axis is at a maximum.
CS'	The point in the median plane on the internal surface of the mandibular symphysis, opposite CS.
CM_1	The point on the lateral surface of the corpus of the mandible, below the centre of the crown of M_1, at the position where the corpus breadth perpendicular to the long axis and parallel to the occlusal plane is at a maximum.
CM_1'	The point on the medial surface of the mandibular corpus, opposite CM_1.
DK (dacryon)	The intersection of the axis of the lacrimal fossa with the fronto-maxillary suture.
EG	The point on the lateral wall of the entoglenoid

	process at the most medial and inferior limit of the articular surface of the mandibular fossa.
EK (ectoconchion)	The intersection of the most anterior surface of the lateral orbital margin with the orbital long axis.
FA (frontomalare anterior)	The most anterior point on the fronto-malar suture.
F.H. (Frankfurt Horizontal)	The plane passing through the most inferior points on the lower orbital margins and through left porion.
FM	The edge of the lateral border of the foramen magnum, at the point at which the width of the foramen in the coronal plane is at a maximum.
FO	The centre of the foramen ovale, at the point of intersection of the maximum antero-posterior and medio-lateral diameters.
FS	The centre of the foramen spinosum (the largest, if multiple foramina are present).
FT (frontomalare anterior)	The point at which the fronto-malar suture intersects the limit of attachment of the temporalis muscle.
GL (glabella)	The most anterior point in the median plane of the bony prominence joining the superciliary ridges.

GN (gnathion)	The most inferior point on the mandibular symphysis, in the midline.
IC	The most inferior point on the posterior margin of the incisive fossa, in the midline.
ID (intradentale)	The most superior point on the alveolar septum between the lower central incisors.
IF	The centre of the infraorbital foramen (the largest, if multiple foramina are present).
IS	The intersection of the infratemporal crest and the spheno-temporal suture.
IT	The most inferior point on the infratemporal crest.
LA (lambda)	The apex of the occipital bone at its junction with the parietals in the midline. Where accessory bones are present this point is located on the general course of the lambdoid suture.
LA'	The point on the endocranial surface of the vault, closest to LA.
LM	The point on the lateral margin of the articular surface of the mandibular fossa, furthest from EG and

on the articular eminence.

M^1B, M^1L etc.	The centre of the alveolar margin on the buccal (lingual etc.) side of M^1.
MF	The centre of the mental foramen.
MP	The point on the lateral aspect of the cranium at which the postorbital diameter reaches a minimum in the horizontal and a maximum in the coronal plane.
MT	Most posterior point on the maxillary tuberosity.
NA (nasion)	The intersection of the fronto-nasal suture with the midline.
NM	The point at which the naso-maxillary suture intersects the piriform aperture.
OC (opisthocranion)	The point on the posterior aspect of the cranium, furthest from GL in the median plane.
O.P. (Occlusal Plane)	The plane that passes with minimum distance from the centres of the occlusal surfaces of all teeth.
PA	The most anterior point on the inferior surface of the petrous temporal bone.

P^4B, P^4L etc.	The centre of the alveolar margin on the buccal (lingual etc.) side of P^4.
PD	The point on the surface of the bony palate, in line with the centres of the second upper molar crowns and in the midline.
PM	The most lateral point on the margin of the piriform aperture, at the junction of the interior and exterior surfaces.
PO (porion)	The most superior point on the upper margin of the external auditory meatus.
PT (pterion)	The most inferior point on the parieto-frontal suture.
PX	The most posterior point on the cranium.
SB	The intersection of the inferior edge of the sphenoccipital synchodrosis with the midline.
S.P. (Sagittal Plane)	The plane perpendicular to F.H. passing through AL and OS.
SS (subspinale)	The deepest point seen in the profile of the naso-alveolar clivus (*H. sapiens*), or the intersection of the plane of the margins of the piriform aperture

	with the naso-alveolar clivus, in the midline.
TP	The most lateral point on the inferior surface of the tympanic plate.
VX (vertex)	The most superior point on the cranium.
ZM (zygomaxillare)	The most inferior point on the zygomaxillary suture.
ZO (zygoorbitale)	The intersection of the orbital margin with the zygomaxillary suture.
ZR	The point on the anterior margin of the posterior zygomatic root, furthest from ZM.
ZY (zygion)	The point on the lateral surface of the zygomatic arch, midway along the zygomatico-temporal suture.
ZY'	The point on the medial surface of the zygomatic arch, closest to ZY.

APPENDIX 2 [Contd.]

Definitions of measurements

B1	Breadth across tympanic plates.	TP-TP	
B2	Breadth between carotid canals.	CC-CC	
B3	Breadth between petrous apices.	PA-PA	
B4	Breadth between the foramina ovale.	FO-FO	
B5	Breadth between the infratemporal crests.	IS-IS	
B6	Breadth of mandibular fossa.	EG-LM	
B7	Length of tympanic plate.	TP-CC	
B8	Length of petrous temporal.	PA-CC	
B9	Position of foramen ovale.	FO-CC	
B10	Position of infratemporal crest.	IS-CC	
B11	Length of foramen magnum.	BS-OS	
B12	Breadth of foramen magnum.	FM-FM	
B13	Length of infratemporal fossa.	ZM-ZR	
B14	Breadth of infratemporal fossa.	IT-ZY'	
B15	Opisthion-infratemporal subtense.	OS [IS/IS	
B16	Basioccipital length.	BS-SB	
V1	Parietal thickness at lambda.	LA-LA'	*
V2	Minimum postorbital breadth.	MP-MP	
V3	Biparietal breadth.	BP-BP	*
V4	Biporionic breadth.	PO-PO	*
V5	Cranial length.	GL-OC	*
V6	Frontal sagittal chord.	NA-BR	
V7	Parietal sagittal chord.	BR-LA	
V8	Parietal coronal chord.	BR-PT	

V9	Occipital sagittal chord.	LA-OS
V10	Frontal sagittal arc.	NA^BR
V11	Occipital sagittal arc.	LA^OS *
V12	Auricular height.	VX [F.H.*
V13	Posterior cranial length.	PX [C.P.*
F1	Upper facial breadth.	FT-FT
F2	Middle facial breadth.	ZY-ZY
F3	Lower facial breadth.	ZM-ZM
F4	Breadth between infraorbital foramina.	IF-IF
F5	Breadth across orbits.	EK-EK
F6	Orbital breadth.	EK-DK
F7	Interorbital breadth.	DK-DK
F8	Lower nasal bone breadth.	NM-NM
F9	Breadth of pirifrom aperture.	PM-PM
F10	Facial height.	NA-AL
F11	Height of infraorbital foramen.	IF-P^4B
F12	Height of orbital margin.	ZO-P^4B
F13	Upper malar height.	FT-M^3B
F14	Lower malar height.	ZM-M^3B
F15	Upper facial prognathism.	PO-GL
F16	Lower facial prognathism.	PO-AL
F17	Malar prognathism.	PO-ZM
F18	Naso-frontal subtense.	NA [FT/FT
F19	Maxillary subtense.	SS [ZM/ZM
M1	Mandibular symphysis height.	GN-ID
M2	Mandibular corpus height at M_1.	M_1B-BM_1
M3	Mandibular corpus height at M_3.	M_3B-BM_3
M4	Height of foramen spinosum.	FS-GN

M5	Height of mental foramen.	MF-BF
M6	Mandibular symphysis depth.	CS-CS'
M7	Mandibular corpus breadth at M_1	CM_1-CM_1'
M8	Breadth between lower canines.	C_1L-C_1L
M9	Breadth between lower second molars.	M_2L-M_2L
M10	Lower incisor alveolar length.	ID-I_2D
M11	Lower premolar alveolar length.	P_3M-P_4D
M12	Lower molar alveolar length.	M_1M-M_3D
M13	I_1 M-D	
M14	I_1 B-L	
M15	C_1 M-D	
M16	C_1 B-L	
M17	P_3 M-D	
M18	P_3 B-L	
M19	M_1 M-D	
M20	M_1 B-L	
M21	M_3 M-D	
M22	M_3 B-L	
P1	Maxillo-alveolar length.	AL [MT/MT
P2	Maxillo-alveolar breadth.	M^2B-M^2B
P3	Breadth between upper canines.	C^1L-C^1L
P4	Breadth between upper second molars.	M^2L-M^2L
P5	Palate depth at incisive fossa.	IC [C^1L/C^1L
P6	Palate depth at second molars.	PD [M^2L/M^2L
P7	Maxillary alveolar subtense.	AL [C^1L/C^1L
P8	Upper incisor alveolar length.	AL-I^2D
P9	Upper premolar alveolar length.	P^3M-P^4M
P10	Upper molar alveolar length.	M^1M-M^3D

P11	I^1 M-D	
P12	I^1 B-L	
P13	C^1 M-D	
P14	C^1 B-L	
P15	P^3 M-D	
P16	P^3 B-L	
P17	M^1 M-D	
P18	M^1 B-L	
P19	M^3 M-D	
P20	M^3 B-L	
A1	Angle of mandibular symphysis.	GN/ID < O.P. (p-i)#
A2	Petro-tympanic angle.	PA/CC < CC/TP (a-l)
A3	Angle of mandibular fossa.	EG/LM < S.P. (a-l)
A4	Angle of foramen magnum.	BS/OS < F.H. (a-s)
A5	Basioccipital angle.	SB/BS < BS/OS (a-s)
A6	Angle of nuchal plane.	OS/LA < F.H. (p-s)
A7	Frontal angle.	NA/BR < F.H. (p-s)
A8	Coronal suture angle.	BR (PT < BR (PT (a)
A9	Lambdoid suture angle.	LA (AS < LA (AS (p)
A10	Subnasal angle.	SS/AL < O.P. (p-s)

See note 3.

KEY TO APPENDIX 2 NOTATION

*	Measurement excludes cranial crests, if present.
AA'	Point on internal aspect of bone, closest to the point AA defined on the external surface.
AA-BB	Length of chord from AA to BB.
AA^BB	Length of arc from AA to BB.
AA/BB	Line from AA to BB.
AA (BB	Arc from AA to BB.
AA [BB/CC	Distance subtended by AA from line BB/CC.
AA/BB < CC/DD	Angle betwen AA/BB and CC/DD.

Notes:

1/ Directional terms (superior, inferior, lateral etc.) refer to an orientation relative to the axes determined by the Frankfurt Horizontal (cranium) or the occlusal plane (palate, mandible).

2/ Dental measurements (M13 to M22 and P13 to P20) are buccolingual and mesiodistal dimensions of the crown, taken parallel to the occlusal plane and parallel or perpendicular to the tooth row.

3/ Angles open anteriorly (a), posteriorly (p), anterolaterally (a-l) anterosuperiorly (a-s), posteroinferiorly (p-i) and posterosuperiorly (p-s).

APPENDIX 3: RAW MEASUREMENTS OF FOSSIL HOMINIDS...CRANIA

	OH 13	OH 24	ER1470	ER1805	ER1813	SK847	Stw53	Sts 5	Sts71
B01	–	[102]	–	(114)	(106)	–	–	90.5	–
B02	–	46	–	50	(42)	–	–	48	–
B03	–	26	–	20	–	–	–	23	–
B04	–	49	–	44	(32)	–	–	47	–
B05	–	65	(82)	76	(70)	–	–	73	–
B06	24	24	28	26	27	27	23	29	26
B07	–	28	–	35	–	25	31	22	–
B08	–	22	–	26	–	21	21	23	–
B09	–	20	–	23	–	21	–	21	–
B10	–	(37)	(50)	46	44	38	–	40	–
B11	–	(29)	–	–	–	–	–	29	–
B12	–	(25)	–	–	–	–	–	25	–
B13	–	–	–	–	45	60	–	53	45
B14	–	–	–	–	–	27	–	31	26
B15	–	–	–	83	(64)	–	–	70	–
B16	–	–	–	–	–	–	–	21	–
V01	5	5	9	8	6	6	6	5	6
V02	–	[76]	82	87	69	–	[71]	66	[54]
V03	–	–	121	105	100	–	–	95	–
V04	–	[118]	132	(115)	109	–	–	99	–
V05	–	–	166	–	146	–	–	147	128
V06	–	–	92	–	80	–	–	76	76
V07	79	76	90	85	77	–	–	86	70
V08	–	–	78	71	69	–	–	62	57
V09	66	(68)	–	(62)	78	–	–	57	64
V10	–	–	106	–	90	–	–	87	87
V11	78	–	–	(78)	96	–	–	70	75
V12	–	–	93	86	71	–	–	72	70
V13	–	73	81	62	73	–	(61)	49	55
F01	–	–	119	–	98	[98]	[86]	92	[81]
F02	–	–	–	–	–	[122]	–	127	[122]
F03	–	–	[108]	–	[86]	[96]	–	103	[102]
F04	–	–	–	–	[52]	–	46	46	50
F05	–	[96]	111	–	90	[96]	–	91	[80]
F06	–	–	43	–	36	41	–	39	35
F07	–	–	23	–	20	[18]	–	17	18
F08	–	–	10	–	9	12	8	9	–
F09	–	–	30	–	23	–	24	27	(27)
F10	–	–	93	–	67	82	–	75	73
F11	–	–	–	–	33	–	(30)	42	37
F12	–	–	60	–	46	–	–	54	48
F13	–	–	91	–	72	72	–	84	72
F14	–	–	–	–	25	27	–	43	35
F15	–	–	120	–	98	–	–	111	91
F16	–	–	(114)	–	117	–	–	147	117
F17	–	–	–	–	70	–	–	84	74
F18	–	–	12	–	10	–	–	11	12
F19	–	–	–	–	10	–	–	24	(25)

APPENDIX 3 [Contd.] ... CRANIA

	ALcom	ER732	ER406	OH 5	SK 46	SK 48	SK 52	TM1517	ER3733
B01	110	-	135	122	-	-	-	-	(125)
B02	59	-	63	59	-	-	-	-	(56)
B03	(48)	-	23	24	-	-	-	-	(28)
B04	62	-	58	58	-	-	-	-	(50)
B05	-	-	(78)	73	-	-	-	-	81
B06	32	31	40	38	33	34	-	33	33
B07	29	-	37	32	28	27	-	35	33
B08	26	-	31	(28)	-	-	-	-	30
B09	22	-	29	19	-	-	-	22	23
B10	-	-	(48)	40	-	-	-	42	46
B11	-	-	(28)	25	-	-	-	-	35
B12	33	-	32	26	-	-	-	-	(32)
B13	-	54	71	(80)	-	62	62	67	45
B14	-	-	50	(45)	-	-	-	-	33
B15	-	-	81	69	-	-	-	-	84
B16	-	-	30	22	-	-	-	-	27
V01	6	(4.5)	-	6	5	-	6	-	(7)
V02	-	61	63	68	[70]	71	-	-	92
V03	96	91	95	106	-	-	-	-	132
V04	128	-	132	137	-	(118)	-	-	131
V05	-	-	163	166	-	-	-	-	182
V06	-	71	73	-	-	(74)	-	-	99
V07	-	-	100	-	-	-	-	-	85
V08	-	-	55	-	-	-	-	-	81
V09	(60)	-	64	58	-	-	-	-	89
V10	-	80	84	-	-	(83)	-	-	112
V11	(72)	-	73	67	-	-	-	-	116
V12	-	66	67	72	-	-	-	-	83
V13	-	-	54	59	-	-	-	-	93
F01	-	[98]	112	112	-	102	-	-	119
F02	-	-	180	(166)	-	-	-	-	138
F03	95	[107]	117	(114)	-	107	[98]	-	100
F04	-	[48]	62	62	[55]	60	[52]	[48]	-
F05	90	[92]	108	106	[112]	102	-	-	114
F06	-	40	43	40	-	42	-	-	46
F07	-	15	26	24	-	25	-	-	20
F08	-	7	15	15	-	-	-	-	17
F09	22	-	28	30	[28]	31	23	-	(31)
F10	-	-	(91)	109	-	-	-	-	85
F11	-	29	51	46	33	38	35	33	-
F12	-	48	60	77	-	62	50	55	(57)
F13	-	-	97	102	-	92	77	-	80
F14	-	-	-	44	-	49	39	-	38
F15	-	106	126	129	-	106	-	-	117
F16	-	-	(160)	166	-	136	141	-	136
F17	-	85	-	115	-	88	97	103	79
F18	-	-	14	12	-	14	-	-	10
F19	-	-	-	(15)	-	14	16	-	20

APPENDIX 3 [Contd.] ... CRANIA

	ER3883	Ndutu	OH 9	Sang4	Bodo	Kabwe	Petra	Arago	Singa
B01	115	-	119	110	-	[120]	-	-	112
B02	52	-	67	46	[66]	[60]	-	-	62
B03	29	-	35	28	[40]	(33)	-	-	(28)
B04	53	-	56	42	[70]	(52)	-	-	54
B05	83	77	70	-	(106)	(88)	-	-	85
B06	28	28	35	30	-	30	30	-	(27)
B07	34	-	30	33	-	30	-	-	26
B08	27	-	24	22	28	22	-	-	24
B09	22	-	23	27	21	19	-	-	19
B10	48	-	53	-	46	33	-	-	36
B11	30	36	-	40	-	-	41	-	(35)
B12	27	29	-	29	-	-	31	-	(30)
B13	-	-	-	-	-	46	40	-	-
B14	39	-	-	-	-	34	27	-	-
B15	73	67	-	-	-	-	-	-	76
B16	21	-	-	21	-	23	-	-	26
V01	(8)	8	(9)	9	13	9	-	12	8
V02	88	-	100	-	110	103	108	104	104
V03	133	135	135	132	151	(146)	150	115	(155)
V04	126	124	134	125	[142]	[132]	148	-	126
V05	184	-	206	-	-	(207)	208	-	192
V06	101	-	-	-	125	121	108	105	120
V07	85	-	-	89	-	111	106	98	95
V08	75	-	-	79	101	90	86	92	97
V09	77	85	-	81	-	(87)	91	-	104
V10	112	-	-	-	144	139	127	115	136
V11	110	111	-	108	-	-	127	-	133
V12	95	92	100	87	116	107	110	-	(114)
V13	75	-	80	92	-	105	108	-	(89)
F01	120	[108]	-	-	139	131	132	123	[126]
F02	[150]	-	-	-	-	[143]	162	-	[140]
F03	-	-	-	-	[136]	113	125	112	-
F04	[52]	[57]	-	-	[82]	72	78	64	-
F05	111	-	119	-	133	124	126	117	[118]
F06	47	-	-	-	53	53	48	45	50
F07	20	22	-	-	32	28	34	25	27
F08	11	[17]	-	-	19	18	15	-	-
F09	-	27	-	-	(40)	30	38	30	-
F10	-	-	-	-	91	94	97	83	-
F11	-	-	-	-	43	44	44	40	-
F12	-	-	-	-	60	59	66	51	-
F13	-	-	-	-	94	91	88	73	-
F14	-	-	-	-	39	32	35	38	-
F15	126	-	-	-	139	130	134	-	123
F16	-	-	-	-	(159)	143	142	-	-
F17	-	-	-	-	90	72	70	-	-
F18	13	-	-	-	23	24	21	13	24
F19	-	-	-	-	-	35	-	38	-

APPENDIX 3 [Contd.] ... CRANIA

	OH 13	OH 24	ER1470	ER1805	ER1813	SK847	Stw53	Sts 5	Sts71
P01	-	(62)	-	70	63	70	(66)	(72)	(67)
P02	(64)	65	-	(69)	64	[60]	(65)	(65)	-
P03	-	31	33	(29)	28	26	24	29	28
P04	(35)	37	-	(42)	36	[26]	31	37	-
P05	-	-	14	-	10	11	8.5	13	9
P06	-	13	-	-	14	12	10	18	-
P07	-	-	7	9	8	5	6	8	7
P08	-	-	18	16	15	14	14	14	14
P09	16	17	17	16	16	(14)	15	14	18
P10	37	37	-	41	34	(32)	36	37	42
P11	-	-	-	(9)	(8)	-	-	-	-
P12	-	-	-	7	6	-	-	-	-
P13	-	-	-	9	9	-	-	-	-
P14	-	-	-	10	8.5	-	-	-	-
P15	(9)	9	-	8	(8.5)	-	-	-	9
P16	11.5	12	-	12	11	-	-	-	(13)
P17	13.5	13	-	13	12	-	(12)	-	(12)
P18	12.5	13	-	13.5	12.5	-	13	-	14
P19	(13)	12.5	-	15	12	(13)	(14.5)	-	15
P20	(13)	14	-	14	13	15	16	-	15

	ALcom	ER732	ER406	OH 5	SK 46	SK 48	SK 52	TM1517	ER3733
P01	73	-	(79)	81	70	69	-	76	-
P02	66	-	76	78	70	68	[68]	[64]	65
P03	31	-	-	31	28	28	30	-	36
P04	33	-	34	38	36	(40)	(34)	-	35
P05	7	-	10	15	7.5	-	-	-	19
P06	12	-	15	22	12	-	-	-	18
P07	11	-	-	5	2	4	(6)	(4)	7
P08	14	-	(12)	16	13	14	16	-	18
P09	17	-	23	22	20	19	21	19	14
P10	40	(40)	49	48	38	39	(43)	38	-
P11	(12)	(7.5)	-	(9.5)	-	-	-	-	-
P12	8.5	-	-	8	-	-	-	-	-
P13	(10)	-	-	8.5	-	8	-	-	-
P14	10	-	-	9.5	-	9	-	-	-
P15	(9.5)	-	-	11	-	9	10	10	(10)
P16	12	-	-	16	-	14	15	14	12
P17	(12.5)	-	(14)	15	(12)	12.5	14	13	12.5
P18	13.5	-	21	17.5	15	14	17	14.5	13
P19	(15)	-	-	16	15	13	16	14	-
P20	14.5	-	-	20.5	16.5	16	16.5	16	-

APPENDIX 3 [Contd.] ... CRANIA

	ER3883	Ndutu	OH 9	Sang4	Bodo	Kabwe	Petra	Arago	Singa
P01	-	-	-	76	72	69	66	66	-
P02	-	-	-	79	(77)	77	78	73	-
P03	-	-	-	37	39	34	35	31	-
P04	-	-	-	43	[48]	49	49	42	-
P05	-	-	-	15	-	10	10	10	-
P06	-	-	-	20	21	19	12	18	-
P07	-	-	-	15	4	8	8	11	-
P08	-	-	-	19	18	18	19	19	-
P09	-	(14)	-	19	16	15.5	18	16	-
P10	-	-	-	39	36	31	37	31	-
P11	-	-	-	-	-	-	-	-	-
P12	-	-	-	-	-	9	-	-	-
P13	-	-	-	9.5	-	10	10	-	-
P14	-	-	-	11.5	-	11	9	-	-
P15	-	-	-	(9.5)	-	(8.5)	8	(9)	-
P16	-	-	-	12.5	-	11	12	10.5	-
P17	-	-	-	(13)	-	(12)	12	(12)	-
P18	-	-	-	13.5	-	14	13	12.5	-
P19	-	-	-	(11)	-	(9.5)	10	9.5	-
P20	-	-	-	14	-	12.5	13	11	-

APPENDIX 3 [Contd.] ... MANDIBLES

	OH 7	OH 13	OH 22	ER730	ER992	ER1802	ER1805	ER3734	SK 15
M01	-	27	33	33	38	38	-	-	(31)
M02	-	24	28	33	32	37	31	33	28
M03	-	27	29	32	33	33	-	28	26
M04	-	14	15	16	16	(18)	-	-	-
M05	-	14	17	15	17	18	-	18	17
M06	-	17.5	20	18	23	21	22	-	16
M07	22	17	20.5	19	20	20	22	19.5	19
M08	(25)	19	-	20	22	19	(18)	-	18
M09	-	35	-	[38]	-	36	42	-	(38)
M10	13	9	11.5	10	13	10	(10)	-	9
M11	20.5	17	18	16	18	18	(17)	16	17
M12	-	40	39	(38)	38	-	(44)	41	41
M13	(7)	-	-	-	-	-	-	-	-
M14	7	-	-	-	-	-	-	-	-
M15	8.5	8	7.5	-	(10)	-	-	8	-
M16	9	9	(9)	-	9	-	-	6	-
M17	9.5	(9.5)	10	-	10	11	-	9	9
M18	9.5	9	10	-	11	12	-	8	10
M19	14	(13.5)	(13.5)	(12)	(12.5)	(15.5)	-	(14)	(13)
M20	12	11.5	12	12	11	13	-	(11)	12
M21	-	14.5	-	(14)	(13.5)	(18)	15	-	14.5
M22	-	12.5	-	11	12	(14)	12.5	-	12

APPENDIX 3 [Contd.] ... MANDIBLES

	BK 67	BK8518	Zh.H1	Zh.K1	Sang1	Sang9	Arag2	Arag13	Mauer
M01	-	29	33	34	32	41	30	38	35
M02	33	26	26	25	34	36	30	31	33
M03	34	28.5	28	26	33	33	28	28	29
M04	14	12	12	9	15	-	10	14	13
M05	18.5	16	14	14	20	17.5	11	12	16
M06	19	17.5	13	12	17	19	14	20	18
M07	17	21.5	14	15.5	16.5	23	15	22	20
M08	24	18	-	-	-	22	24	-	22
M09	36	40	-	-	-	-	50	-	41
M10	9.5	8.5	10	12	-	10.5	12	11	10
M11	18	19	14	16	17	17	14	19	15
M12	37	39	32	39	41	42	35	41	37
M13	-	-	-	-	-	-	-	-	(6)
M14	-	6	-	-	-	-	-	-	7.5
M15	-	10	-	(9)	-	(8)	-	-	(8.5)
M16	-	10	-	9	-	(9)	-	-	9
M17	-	-	(8)	(10)	-	9	-	9	(8)
M18	-	-	(9.5)	10	-	11	-	11	9
M19	(11)	(12)	-	(13)	(13)	-	(11.5)	(14.5)	(12.5)
M20	11	11	-	12	13	-	11	13	11.5
M21	13	(14.5)	11	-	14	(14)	(11.5)	13	(12.5)
M22	11.5	11.5	10	-	12.5	13	10	12.5	11

	SK 12	SK 23	SK 34	TM1517	ER1482	ER 729	ER 818	ER3230	Peninj
M01	50	47	43	-	40	(55)	(61)	(52)	45
M02	42	38	39	36	34	46	53	41	39
M03	38	35	36	35	30	47	49	-	34
M04	15	15	-	-	14	23	31	25	20
M05	26	22	19	20	20	33	33	29	19.5
M06	28	26	19	-	20	29	(30)	24	24
M07	31	24	21	23	20	28	35	28	27
M08	20	19	-	-	17	20	-	(22)	20
M09	-	-	-	-	(35)	50	-	41	46
M10	11	10	10	(8)	16	11	10	12	11
M11	21	20	18	21	18	24	27	26	22
M12	48	48	48	47	44	55	59	58	50
M13	-	5.5	6	-	-	5	-	5.5	6
M14	-	6	6.5	-	-	8	-	7	6
M15	-	8	8	9	-	8	-	8	7
M16	-	8	9	9	-	10	-	10	8
M17	-	9	10	10	-	(12.5)	-	11	9.5
M18	-	11.5	13	12	-	13	-	14	13
M19	-	14	14	(15)	14	(16)	(18)	(17)	16.5
M20	-	15	14	13	14	16	-	16	14.5
M21	17	16	17	16	(17)	22	(22)	21	18
M22	15.5	14	16	14	15	19	(19)	17	15

APPENDIX 3 [Contd.] ... MANDIBLES

	Sts 7	Sts 36	Sts 52	MLD 18	MLD 40	LH 4	AL 128	AL 198	AL 266
M01	43	40	36	-	38	(41)	34	40	32
M02	38	35	28	35	36	32	-	33	31
M03	32	33	(26)	31	35	(28)	-	31	29
M04	-	-	14	-	16	15	11	-	-
M05	22	17	15	-	21	19	14	15	12.5
M06	(23)	(18)	18	(22)	21	19	18	19	20
M07	(24)	20	(20)	20	24	19.5	18.5	15.5	18
M08	21	20	19	18	-	21	-	-	27
M09	-	-	(39)	-	-	34	-	-	36
M10	11	9	11	10	(10.5)	11	-	11.5	9
M11	19	18	19	17	18	19	16	15.5	18
M12	43	42	42	40	45	43	39	36	45
M13	-	-	6.5	4.5	-	-	-	-	-
M14	-	-	7	6	-	-	-	-	-
M15	10	9.5	9	9	8	8	7.5	8.5	-
M16	11	11	10	9	9	11	8.5	8.5	-
M17	-	12.5	9	(8.5)	9	(11)	(8)	(9)	(9.5)
M18	13	13	12	12	11	10.5	9	10	10.5
M19	-	-	14	(13.5)	(13)	(12.5)	(11.5)	(10.5)	(13)
M20	-	-	13	13	12	12.5	11	(12)	12.5
M21	(16)	16	14	(15)	-	(16.5)	13	(15)	(16)
M22	15	16	13	14	-	14	12	13	14

	AL 277	AL 288	AL 333	AL 400
M01	42	32	48	41
M02	39	30	40	35
M03	-	27	-	-
M04	14	11	12	13
M05	17.5	13	17	15
M06	18	18	21.5	19.5
M07	18	18	23	19
M08	-	16	23	21
M09	-	29	-	33
M10	10	8.5	12	11
M11	18	14	19	16
M12	-	39	44	43
M13	-	-	-	(6.5)
M14	-	-	-	8
M15	(8.5)	-	-	(8)
M16	11.5	-	-	9
M17	(10)	8	(10.5)	(10)
M18	12	10	12	11
M19	(12.5)	(12)	(15)	(13)
M20	(13)	11	14	13
M21	-	14.5	(15.5)	(15)
M22	-	12	14.5	14

APPENDIX 4

Raw measurements of extant primates and modern humans

Note: Locations of specimens are given in Appendix 1; definitions of measurements are given in Appendix 2.

Key:

Col - *Colobus*

Pap - *Papio*

Hyl - *Hylobates*

Pon - *Pongo*

Gor - *Gorilla*

Pan - *Pan*

Hom - *Homo*

Col (f)	3077	3069	3015	3094	3061	3044	3013	3066	3045	3042
B1	63	59	56	58	57	56	52	50	56	59
B2	27	26	25	24	26	25	25	23	26	26
B3	13	14	12	12	13	12.5	12.5	11	13	13
B4	30	29	29	28	30	29	29	28	29	31
B5	43	39	37	39	42	41	37.5	37	37.5	42
B6	15	15	14	15	16	14	12	13	13	16
B7	18	17	16	17	15	16	14	13	15	17
B8	16	14	15	15	13	14	14	14	15	16
B9	13	14	12	14	13	12	11	10	12	14
B10	25	22	25	23	23	22	22	20	23	23
B11	17	13	16	14	14	13	16	18	15	16.5
B12	17	15	16	14	15	16	15.5	16	16	16.5
B13	35	30	33	30.5	32	30	31.5	28	33	33
B14	25	23	24	23	24	23	22	20	21	24
B15	41	37	42	37	39	36.5	39	38	40	38
B16	15	15	15	15.5	16	15	13	13	15	15
V1	1	1	1	1	1	1	1	1	1	1
V2	45	45	42	42	47	43	42	44	45	46
V3	58	55	57	54	56	53	53	54	55	56
V4	62	59	58	59	58	57	53.5	51	56	59
V5	83	79	76	76	78	76	75	73	76	79
V6	49	51	46	45	50	45	50	45	47	47
V7	40	36	36	37	36	34	35	37	39	39
V8	36	37	37	35	38	33	32	34	37	32
V9	23.5	26	24	23	23.5	22	23	20	21	23
V10	50	53	49	46	52	48	52	47	52	49
V11	26	29	27	28	27	26	23	23	23	26
V12	37	40	39	37	38	36	39	36	39	38
V13	26	23	23	25	22	25	24	26	22	23
F1	60	63	59	57	60	57	54	52	57	60
F2	80	74	74	71	77	72	71	64	71	74
F3	58	52	54	51	53	50	49	46	45	55
F4	28	27	28	25	23	26	27.5	24	25	27
F5	55	58	54	53	57	55	50.5	49	54	57
F6	24	25	24	24	24	24	22.5	22	23	24
F7	11	12	10	10	11.5	12	10	8.5	10	12
F8	7	8	6.5	7	9	8.5	7.5	6.5	7	8
F9	13.5	11	12	13	11	11	10.5	9	11	12
F10	43	38	37	41	39	38	36	34	34	41
F11	18	17	15	18	18	15.5	13	14	15	18.5
F12	22	19	19	19	19.5	17.5	17	15.5	18	20
F13	39	34	35	35	37	33.5	34	29	35	37.5
F14	15	14	16	14	14	14	14	13	14	15
F15	68	66	64	64	66	63	61	58	64	66
F16	90	80	82	86	82	79	81	74	82	87
F17	50	46	48	45	48	44	46	44	49	51
F18	11	13	10.5	13	11	11	10	11.5	10	11
F19	28	27	26	29	24	25	27.5	22	24	25

Col (f)	3077	3069	3015	3094	3061	3044	3013	3066	3045	3042
M1	26	24	26	24	22	22	24	22	22	24
M2	21	22.5	20	20	20	18.5	18	16.5	17.5	22
M3	20	21	20	21.5	21	18	19	17	19.5	22
M4	8	8	8	7	9	8	8	7	8	8
M5	8	7	9	8	7.5	7.5	7	7	7	7.5
M6	10.5	12	9.5	10.5	9.5	11	10.5	8.5	10	11
M7	7	8	8	7	8	8	7	7	9	7.5
M8	12	10	11	11	11.5	11	10	8	11	11
M9	21	18	20	20	19	19	19	16.5	18	18
M10	7	7	6	7	6	7	7	6	7	7
M11	14	13	13.5	12	14	14	13	13	13.5	14
M12	24	24	23	24	24	25	24	26	24	24
M13	4	3.5	3	4	3	4	4	4	3.5	4
M14	4	4	4	4	4	4	4.5	4	4	4
M15	6	6	6	5.5	6	6	7	6	6	6
M16	6	6.5	6.5	6	6	6	6	6	6	6
M17	8	7.5	7.5	6.5	8	8	7	6.5	7	7
M18	5.5	7	5	5	5	6	6	6	5	5
M19	7	7	7	7.5	7	7	6.5	7	7	7
M20	5.5	5.5	5.5	5.5	6	5.5	5.5	5.5	5.5	5
M21	10	10	9	10	9.5	9	9	10	10	10
M22	6.5	7	6.5	6	6.5	7	6.5	7	6.5	7
P1	50	46	44	49	45.5	43	45	44	45	49
P2	37	34	32	34	35	36	34	32	34	35
P3	17	18	17	17	16	16	14	14	15	18
P4	24	20	17	20.5	21	21	21	17.5	21	20
P5	5	5	5	4	4.5	4.5	4	4	3	4
P6	7	6.5	6	6.5	8	7	6	5.5	6	6
P7	8	7.5	7.5	9	7	7	8	7	8	8
P8	9	8.5	8	9	8	10	9	9	9	9
P9	10.5	10	10	10	10.5	11	10	10.5	10	11
P10	22	21	20	22	21	21	20	22	21.5	22
P11	5	5	4	5	5	5.5	5.5	4.5	5	5.5
P12	4	4.5	4	4.5	4	4.5	4	4	4	4.5
P13	8	7	6	6.5	7	7.5	8	7	7	6.5
P14	6	6	5	5	6	6	6.5	5	5.5	5.5
P15	5.5	5	5	5	5.5	6	5	5	5	6
P16	5.5	6	5	5	6	6	6	5.5	5	5.5
P17	7	6.5	6.5	7	7	7	7	7	7	7
P18	6	6.5	7	6.5	6.5	6.5	6	7	6.5	6
P19	8	8	6	8	7.5	7	7	8	7.5	7.5
P20	7	7	7	7	7.5	7	7	7	7	7

Col (m)	3071	3084	3078	3067	3081	3059	3055	355	3052	3063
B1	65.5	58	60	63	56	61	63	62	67	63
B2	27	24	24	27	25	26	27	26	28	27
B3	15	12	14	14	14.5	14	13	14	14.5	14
B4	32	29	28	31	29	30	33	30	31	32
B5	42	42	39.5	42	35	45	45	42	45	39
B6	18	15	16	15.5	14.5	16	16	16	18	17
B7	19	16	18	18	16	18	18	18	19	18
B8	15	15	15	17	13.5	16	16	15.5	17	16.5
B9	16	13	15	14.5	13	14	17.5	14	20	17
B10	23.5	21.5	24	26	23.5	24	24	24.5	24	25
B11	16	13	13	13.5	15	15	16	15	14	14
B12	17	16	15.5	16	17	16	18	18	16	15
B13	32.5	31	33	35	30	34	35	36	36	36
B14	24	22.5	26	24	21	26.5	23	27	29	26
B15	41	36	40	41	40	38	39	44	41	40
B16	15	17	19	17.5	15	18	18	19	19.5	19
V1	1	1	1	1	1.5	2	2	2	2	1.5
V2	45	46	44	44	43	46	48	44	47	47
V3	58	56	56	55	55	58	58	56	62	58
V4	66	59	62	66.5	57	64	64	62	70	63
V5	83	78	83	82	76	80	81	82	85	83
V6	47.5	48	47	50	47	50	51	54	50	50
V7	42	35	37	37	35	38	37	34	38	38
V8	34	34	36	36	32	34	35	32	41	38
V9	22.5	24.5	25	25	25	25	27	27	25	25
V10	50	52	49	51	49	51	52	55	52	52
V11	23.5	27	30	28	28	29	28	31	31	30
V12	36	41	36	41	37	42	38	39	41	40
V13	24	18	23	22	26	26	23	23	24	25
F1	58.5	60	63.5	63	56	62	66	68	70	68
F2	75.5	76	79	80	70	81	80	84	88	82
F3	57	53	56	52.5	49	57	53	56	61	57
F4	35.5	34	28	32.5	26	29	30	32	35	31.5
F5	54	56	57	57	52.5	58	60	59	62	61
F6	25	24	23	24	23	24	26	25	24	26
F7	10	12	12.5	12	10	12	13	11.5	15	12
F8	9	9.5	9.5	8.5	6	10.5	6.5	8	14	8
F9	12.5	12.5	13.5	12	11	11	15	14.5	15	13
F10	42	37	44	44	38	39	42	48	49	43
F11	16.5	15	22	18	16	18.5	20	18.5	20	21
F12	21	19	25	23	19.5	21	22	24.5	25	23
F13	36.5	36	39	39.5	34	42	42	37	42	40
F14	14	14	15	14	14.5	17.5	16	14	19	17
F15	68	66	69	68	61	69	72	70	73	70
F16	89	85	91	90	79	90	92	97	96	93
F17	47.5	47	50	50	45	50	51	53	54	52
F18	12	11	12	12	10	11	12	11	12	10
F19	32	31	32	31	25	30	31	34	36	32

Col (m)	3071	3084	3078	3067	3081	3059	3055	355	3052	3063
M1	28.5	25.5	29	30	22.5	25	29	31	31	33
M2	22	20	26	24	19	22	23	23	24.5	26.5
M3	20	21	25	22	18	21	24.5	21	26	23
M4	10.5	8	10	9.5	7	9	10	9	10	11
M5	8.5	8	9	8	8	8	8.5	9	10.5	11
M6	11.5	11	14.5	14	11	12	12	13	14	13
M7	8	7.5	8.5	9	8	8	9	9	10	9
M8	10.5	10.5	13	12	10	10.5	11.5	13	13	13
M9	19	18	20	20	19	18.5	20	21	22	22
M10	5	6.5	7	7	7	6	6.5	6.5	7	7
M11	14	15.5	15.5	15	12	13	14.5	14	14	15
M12	26	24	26	25	24	24	28	28	25	24
M13	4	3.5	3.5	4	3.5	3	4	4	3.5	4
M14	5	4	4.5	4	4	3.5	4	5	4	4
M15	7	8	7	8.5	7	7.5	8	7	8	6.5
M16	7.5	6.5	7.5	8	6.5	6.5	7	7.5	7	7
M17	8	8	8	8	7	8	9	8	8	9
M18	6.5	7.5	7	6	6	6	7	8	6	5.5
M19	8	7.5	7	7.5	7	7	8	8	7.5	7
M20	6	6	5.5	5.5	6	5.5	6	6	5.5	5
M21	10	9	10	9	10	9.5	11	12	9.5	10
M22	7	6	6	7	6	6	7	7.5	7	7
P1	50	49	52	51	45	49	51	54	53	50
P2	37	35	37	38	35	34	38	37	38	38
P3	17.5	17	19	19.5	16	18	19	20	20	22
P4	22	20	22	22.5	21	21	22	22	24	23
P5	3.5	4.5	7	6	4	5	5	6	5	6
P6	7.5	7	7	6.5	6	8.5	7	6.5	7	9
P7	7	7	9	8.5	7	10	8	7	10	9
P8	10	9	10	10	9	9	10	10	10	9
P9	10	11	10.5	10.5	11	10	12	11	10.5	10
P10	23	22	23	22	22	22	24	24	22	21
P11	5	4	5	5.5	5	5	5	5.5	5	5
P12	5	4.5	5	4.5	4.5	4	4	5	4.5	4
P13	10	8	10	9	7	8	9	8.5	8	6
P14	7	5.5	8	7	6	7	7	9	7	7
P15	5.5	6	6	6	5	5	7	5.5	5.5	5
P16	6	6	6.5	6	6	5	6	6	5	5
P17	8	7	7.5	7	7	7	8	7	7	7
P18	7	6.5	7	7	6.5	6	7	7	6	6
P19	8	7.5	8	8	7.5	7.5	8	8	7	8
P20	7.5	7	7	7.5	7	7	8	8	7	7

Pap (f)	3143	3144	3150	3158	3153	3157	442	465	445	426
B1	81	81	76	75	76	77	76	71	79	80
B2	33	33	31	32	31	29	32	29	33	35
B3	15	16	15	14	15.5	14	17	14	13	15
B4	39	41	36	36	38	36	37	34	39	38.5
B5	55	56	53	53	54	56	52	49	53	54
B6	20	18	20	18	17.5	19	21	18	21	21.5
B7	28	28	26	25	26	28	23	23.5	27	26.5
B8	20	17.5	18	18	17.5	17	18.5	17	21	19
B9	15	16	12	13	16	15	17.5	16.5	16	17
B10	26	24	26	24	26	26	27	25	25	27.5
B11	20	21	18.5	22	18.5	21	22	19	19.5	21
B12	18	18	18	18.5	18	17.5	18	18	20	19.5
B13	34	33	36	35	32	39	36	30	36	38
B14	28	27	28	26	26	29	27	27	26	26.5
B15	43	42	45	45	44	43	44	41	44	47
B16	19	17	18	16	15	15	18	17	18	18
V1	3	4	3	3	3	2	2.5	3	2	2
V2	56	57	56	55	56	57	53	53	51	53.5
V3	74	74	77	72	71	74	78	73	72	72
V4	81	79	76	75	75	74	76	75	78	80
V5	97	100	100	97	98	99	100	96	99	100
V6	61	59	58	60	56	58	57	56	62	57
V7	43	44	47	46	50	44	42	43	38	46
V8	45	41	45	45	45	46	41	47	48	48
V9	40	46	40	37	40	43	38	44	41	38
V10	67	65	63	69	63	62	65	63	69	63
V11	42	50	45	44	46	51	46	52	50	43
V12	46	47	46	48	46	45	45	46	43	45
V13	37	35	31	38	34	32	37	37	37	38
F1	72	71	72	69	68	72	72	62	67	69
F2	98	97	97	93	93	97	97	90	98	95
F3	70	70	72	68	72	69	73	67	65	69
F4	41	32.5	41	39	34	35	36.5	32	35.5	36
F5	64	63	63	61	64	66	66	56	60	63
F6	29.5	29.5	29	28.5	29	29	31	26.5	28	30
F7	8.5	8	9	7.5	8	8.5	7	6	8	5.5
F8	10	10.5	10.5	9.5	10	11	12.5	7	10	9
F9	16	16.5	17.5	17	15	17	19	15.5	18.5	17
F10	94	95	99	86	89	91	93	80	98	88
F11	44	40	43	40	41	40	40	37	47	43
F12	56	54	59	51	54	53	53	48.5	60	54
F13	64	61	62	56	61	63	62	56	64	59
F14	22	22	21	19	22.5	19	20	20	21.5	21
F15	78	79	81	76	75	80	79	74	80	78
F16	124	123	131	118	128	129	131	114	132	129
F17	56	54	60	56	55	64	58	50.5	59	61
F18	10	11	10	10	11	8	8.5	10	11	8
F19	50	51	60	46	58	48	52	47	58	51

Pap (f)	3143	3144	3150	3158	3153	3157	442	465	445	426
M1	36	38	37	30	35	34	40	34	33	34
M2	27	29	30	23.5	28	28	28	25	27	26
M3	24	25	27	22.5	23	25	25	21	24	24
M4	11	12	10	11	11	11	12	9	11	11.5
M5	8.5	10	9	10	9	10	11	7	9	10.5
M6	17	16	17	15.5	16	15	16	15	17	19
M7	11.5	11	11	11	10	9.5	11	9.5	12	10.5
M8	16	16	18	16	15.5	17	18	14	17	14
M9	24.5	23	24	22	22	23.5	23	19	23.5	24
M10	11	11	11	11.5	12	12	12	11	11	12.5
M11	16	18	16	16	18	14.5	16	16.5	17	18.5
M12	35	34	24	36	35	35	36	36	39	38
M13	7	6	6	6.5	7	7.5	6.5	6	6.5	6.5
M14	7.5	8	8	7	8	7	7	7	7	7
M15	6	7	7	7	5	6	6	7	7	6
M16	8	8	6	7	8	7.5	7	7	7	8.5
M17	9	10	9	8	10.5	7.5	9	8	9	10
M18	5.5	5	5	5.5	6	5.5	5	6	6	6
M19	10	10.5	10	10	10.5	10	10	10	10	11
M20	8	8	8	8	8	8	8	8	8	8
M21	16	14	14	14	14.5	14	15	15	16	14.5
M22	11	11	10	10	10	9.5	10	10	10.5	10
P1	72	69	72	67	73	69	76	68	71	73
P2	50	48	48	47	48	46	46	43	48	46
P3	22	21.5	26	22	22	23	24	18	23	23
P4	27	27.5	27	25	27	28	27	22	27	27
P5	7	9	8	7	9	8	8	6	12	7.5
P6	10	11	10	7	9.5	10	9	7	9	7.5
P7	15	15	15	16	17	16.5	19	15	14	17
P8	15	15	14	16	16.5	17	16	17	15	18
P9	13	14	13	13.5	14	13	13	14	14	15
P10	33	34	32	34	33	32	33	34	35	34
P11	9	8.5	8	9	9	10	9.5	10	9	11
P12	8	8	8.5	8	8	9	8	8	8	9
P13	8	8	8	8	8	8	7.5	8.5	8	8
P14	7	8	7	7	7	7	7	8	7.5	6.5
P15	7	6.5	7	7	7	7	6.5	7	7	7.5
P16	7	8	8	7	8	8	7.5	7.5	7	8
P17	10	10.5	10.5	10.5	10	10	10	10	11	11
P18	9	10	9	9.5	10	9	9	9.5	9.5	9
P19	12.5	12	12	11	12	11	12	12.5	12	13
P20	11	11.5	11	11	11	10.5	10.5	11	12	11

Pap (m)	6616	3159	6614	3152	3145	3163	3161	3151	6429	6618
B1	90	85	88	92	92	87	91	91	89	83
B2	35	34	36	37	37	37	35	35	37.5	32
B3	16.5	16	19	18	17	17	18	17	18	19
B4	41	42	42	44	43	40	42	43	40	37
B5	57	61	59	64	69	64	56	56	63	62
B6	25	20.5	23	22	25	21	25	22	20	22
B7	28	29	29.5	30	30	28	32.5	31.5	28	27
B8	22.5	21	23	24	24	22	22	23	23	20
B9	22	19	21	19	23	18	23	22	24	16
B10	33	29	29	32	33	30	31	30.5	32	26
B11	22	20	21	23	22	22	20.5	23	21	21
B12	21	19	19	20	19.5	21	18.5	19.5	20	17
B13	44	40	43	46.5	44	44	42	41	42	37.5
B14	36	29.5	30	35	35	35	34	31	35	29
B15	55	47.5	52	55	54	52	54	55	53	49
B16	18	18	19	22	20	19	20	19	21	21.5
V1	3	2.5	4	2	3	2	3	3	4	2
V2	61	55	59	58	59	57	57	56	59	56
V3	76	73	76	74	76	77	76	76	81	68
V4	90	83	88	89	91	89	88	91	91	81
V5	112	103	114	110	115	105	108	110	114	107
V6	62	60	65	64	64	64	64	63	59	60
V7	45	44	52	50	49	43	50	49	55	52
V8	48	46	48	47	45	51	46	46	48	42
V9	46	43	46	39	42	44	44	41	42	37
V10	67	64	70	72	68	71	68	68	64	68
V11	55	49	51	48	51	50	51	50	53	47.5
V12	48	45	47	46	44	46	45	44	47	55
V13	39	31	37	33	36	30	34	39	39	33
F1	84	75	84	89	85	83	83	79	88	88
F2	117	107	108	120	121	118	113	109	117	107
F3	85	77	78	81	86	78	80	81	83	74
F4	44	42.5	48	42	44	45	42	43	43	48
F5	76	71	76.5	78	76	77	84	73	76	78
F6	33	31	34	35	33	34	33	32	34	34
F7	14	9.5	13	13	12	9.5	12	12	10	14
F8	13	11	13.5	13	13	15	11	13	13	17
F9	23	16	26	22	21.5	22	19.5	22	22	23
F10	115	114	118	127	130	127	130	117	113	127
F11	55	55	58	58	58	57	58	51	57	59
F12	71	69	71	77	80	78	77	71	71	76
F13	75	77	75	87	89	81	85	73	75	82
F14	27.5	30	28	33	35	32	33	26	33	31
F15	91	85	93	93	94	90	92	93	95	91
F16	164	154	172	174	168	168	170	160	166	161
F17	73	71	70	78	74	71	76	71	71	64
F18	10	10	13	12	11	10	12	12	8.5	14
F19	66	66	78	70	70	55	71	66	66	68

Pap (m)	6616	3159	6614	3152	3145	3163	3161	3151	6429	6618
M1	55	41	57	48	51	46	46	45	55	55
M2	36	30	38	34	37	34.5	34	31.5	36.5	36
M3	29	26	33	30	29	26	29	27	29	28
M4	14	15.5	12.5	17.5	19	15	15.5	15.5	13	17
M5	6.5	7.5	9.5	11	11	11	11.5	11	12	12
M6	21	25	24	29	25	25	25	24	23	24.5
M7	11.5	12	11.5	11	12	11	11	12.5	11.5	11.5
M8	18	14	17	13	14	15	15.5	16	15	19
M9	30	25	29	27	25	30	26	26	29	23
M10	14	12	12	15	13	12	12	13	12	14.5
M11	29	21	20	28	26	29	25	23	27	28
M12	41.5	41	43	42.5	51	41	39	42	40	40
M13	7.5	8	8	8	7.5	7	7	7.5	8	8
M14	9.5	8.5	9	9	8.5	9	8	8	9	9
M15	11	12	10	13	12	13	12	13.5	12	10
M16	13	12	15	15	15	15	11	13	14	14
M17	23	17	23	20	17	20	17	15	19	20
M18	8	10	7	9	9	9	5.5	9	9	9
M19	11.5	11	12	11.5	11	11.5	11	11.5	11	10.5
M20	9	9	9	9	9	9	9	9	9	8
M21	17	17	17	18	17	16.5	16	16.5	15.5	16
M22	12.5	11	12	12	12	11	11.5	12.5	12	12
P1	98	88	98	99	94	99	96	91	93	96
P2	57	53	58	53	52	54	52	52	55	53
P3	32	23	37	25	26	24	27	26	29	30.5
P4	33	31	32	30	29	31	32	30	31	27
P5	12	7	11	9	9	11.5	10	8	12	12
P6	11.5	8	10	11.5	12	11.5	15	9	11	15
P7	22	22	23	22	21	20.5	25	26	20	23
P8	18	20	19	19	20	20	16	21	19	20
P9	17	15	17	15	16	16	14	15	17	15
P10	39	37	40	39	37	37	36	39	37	37
P11	11.5	11	12	11	12	11	10	12	10.5	11
P12	10	10	10	10	10	11	9	8	10	9
P13	13	14	15	15	13	16	10.5	14	13	18
P14	12	10	15	13	15	13	12	9.5	11.5	13
P15	8	7.5	8	8	8	8	7	8	7.5	7.5
P16	8	8.5	8	8.5	9	9	9	8.5	8.5	9
P17	12	12	12	12	11	12	11	12	12	10
P18	11	10.5	10.5	11	11.5	11	10	10	10.5	10
P19	14	13	14	14	13	13	12	13	13	13
P20	14	13	12.5	13	12	12	12	12	12	14

Hyl (f)	55. 1500	1914.8 .22.1	24.9. 2.7	14.12 .8.7	10.10 .1.7	55. 1498	14.12 8.8	24.9. 2.6	10.10 .1.8	55. 1493
B1	61	61	60	60	59	66	64	68	61	58
B2	20	26	26	23	23	27.5	26	28	27.5	22
B3	13	14	14.5	14	14.5	14	14	14.5	14	16
B4	23	26	23	24	25	27	25	26	26	26
B5	39	42	39	38	38	42	42	41	39	40
B6	12	11	11.5	11	11	12	12.5	12.5	11.5	11.5
B7	22	19	18	20	19	20	20	20	17.5	18
B8	17	14	11	14	15	15	14.5	13.5	17.5	14
B9	15	12	9	12	15	12.5	13	12	15	13
B10	24	21	20	21	23.5	20	24	21	23	22
B11	18	17	16	19	15	16	18	17	17	16.5
B12	16	17	17	16.5	15	16	17	16.5	14.5	15.5
B13	29	31	27	27	26	28	28	30	26	28
B14	18.5	19	16	15	15	21	16	20	18	16
B15	41	40	39	40	37	39	41	40	40	41
B16	16	14	15	14.5	15	16	15	16	15	16
V1	1	1	0.5	1	1	1	0.5	1	0.5	1
V2	48.5	49	46.5	49	48	49	50	51	48	43
V3	61	64	61	58	60	60	63	64	59	58
V4	64	63	63	60	60	66	65	67	62	63
V5	82	80	78	78	74	80	85	83	77	83
V6	57	58	59	58	56	62	59	63	63	59
V7	27	25	29	25	23	27	34	23	23	28.5
V8	45	45	47	44	44	47	45	51	47	–
V9	30	34	27	32	34	35	34	36	29	28
V10	62	62	63	64	61	70	65	72	71	68
V11	36	39	29	36	37	39	38	43	31	31
V12	40	43	44	40	42	43	44	47	42	42
V13	38	33	34	35	31	37	38	34	34	33
F1	66	62	55	58	61	60	61	60	59	60
F2	68	70	67	63	65	73	68	72	65	67
F3	50	50	45	48	49	50	51	50	51	48
F4	26	23	24	24	24	23	28	26	25	25
F5	64	60	55	59	59	59	61	60	61	61
F6	27	25.5	23	25	25	26	24.5	25	26	27
F7	14	12.5	12	11	12	10	15	13	10	11
F8	10	9.5	9	9.5	11	8	9	10	9	9
F9	13	13	14	12	12	10	16	14	13	13.5
F10	34	31	33	26	30	31	34.5	32	32	33
F11	16	14	14	15	15	13.5	16	15	15	14
F12	18	15	16.5	16	15.5	14.5	20.5	18	16	16
F13	34	33	34	35	34	38	40	40	37	36
F14	11	10	8.5	9	10	9	12	11	11	10
F15	61	61	56	58	57	59	61	63	57	63
F16	75	71	71	68	70	71	75	77	70	76
F17	38	38	36	35	36	35	37	39	35	39
F18	6	7	8	7	6.5	6	6	6	5	6
F19	31	27	27	27	26	28	30	28	28	29

Hyl	55.	1914.8	24.9.	14.12	10.10	55.	14.12.	24.9.	10.10	55.
(f)	1500	.22.1	2.7	.8.7	.1.7	1498	8.8	2.6	.1.8	1493
M1	18	17.5	20	16	16	16	19	19	16	16
M2	13	12	13	12.5	13	13	14	13.5	12.5	12
M3	12	11.5	13	11.5	11	12	12	13	11.5	11.5
M4	4.5	4	6	4	3.5	4	4	4.5	4	3.5
M5	5	6	5.5	5	4	4.5	5	6.5	4.5	5
M6	7	6.5	7	6	6	7	6	7.5	7	7
M7	6	6.5	5.5	5	5	6	5.5	6	5.5	5.5
M8	10	11.5	12	10	10	12	10	11	11	13
M9	20	21	20	19.5	21	23	25	19.5	21	22
M10	6	6	6	6	6	6	6	6	6.5	7
M11	10.5	10.5	11	12	11	10	12	11	11	11.5
M12	17	18	18	18.5	17	16	19	19	18	19.5
M13	–	3	3	3	3	3	3	3	3	3
M14	–	3	3	3	3	3	3.5	3.5	3	3
M15	6	5.5	5	5.5	5	6	5.5	5	6	6
M16	5.5	5.5	6.5	6	6	6	7	6	6	6
M17	6	6	6	7	6.5	6	6	6	6	6
M18	4	4	5	4	4	4	4	4	5	5
M19	6	6	6	6	5.5	5	6	6	6	5.5
M20	5	5	5	5	5	4	5	5	5	5
M21	5.5	6	6.5	6.5	5.5	6	6	7	6	–
M22	5	5	5.5	5	5	5	6	5.5	5	–
P1	41	41	42	38	39	41	43	42	41	43
P2	30	32.5	33	32	33	32	34	34	33	32
P3	17	18	19	16	17	18	19.5	19	19	19
P4	18	20.5	20	20	21	22	22	20	21	19
P5	2	2.5	3	3	3	3	3.5	2	2	3
P6	6	6	5	6	6.5	6	8.5	6.5	6.5	5.5
P7	9	10	10	8	7	8	9	8.5	9.5	8.5
P8	10.5	9	9	9	9	8	9	9	9	8.5
P9	9	8.5	8.5	9.5	9	8.5	9	9	9	9
P10	16.5	15	18	17	17	14	16	18	15	17
P11	5	5	4.5	5	5	4	5	5	5	4.5
P12	4	3	4	3.5	3.5	3	4	4	4	3.5
P13	6.5	6	6	7	6.5	7	6	6	7	6
P14	6	6	6	5	5	6	7.5	5	5.5	6.5
P15	5	4	4.5	5	5	5	4.5	5	5	5
P16	5.5	5	4.5	5	5	4.5	5	5	5	5
P17	6	5.5	5.5	5.5	6	5	6	6	5.5	6
P18	6.5	6	6.5	6	6	6	6.5	6	6	6
P19	5	4.5	5.5	5.5	5.5	5	5	6	4.5	5
P20	5.5	5	6.5	6	5.5	5.5	6	6.5	5.5	6

Hyl (m)	14.12 8.1	14.12 8.5	14.12 8.3	14.12 8.6	55. 1497	14.12 8.2	14.8. 22.2	55. 1494	24.9. 2.3	24.9. 2.2
B1	64	62	62	60	60	66	64	62	65	60
B2	26	26	25	25	26	22	26	27	27	26
B3	15	13	14	13	13	16	15	12	15	13
B4	25	26	24	23	25	25	27	26	27	25
B5	38	41	39	39	40	38	43	41	43	42
B6	13	12	13	13	12.5	13	12	12	13	10
B7	21	19	19.5	18.5	17	24	19	19	19	18
B8	16.5	15	15.5	14.5	13	14	13	15	16	13
B9	14	14	14	13	11	14	13	15	11.5	9
B10	23	21.5	22	19.5	18.5	24	23	22	20	18
B11	18.5	18	17	17	17	18.5	17.5	15	19	16
B12	16.5	15.5	15	16	15	17	17	14	18	17
B13	29.5	30	28	30	26.5	29	30	30	31	29
B14	18	18	19	18	19	21	18	17	20	19
B15	44	39	39	39	37	43	41	39	41	37
B16	18	14.5	15.5	14	13	17	15	17	16	16.5
V1	1	1	1	1	1	1	0.5	1	1	0.5
V2	50	47	54	48	49	47.5	50	51	49	44
V3	63	62	64	62	59	60	60	63	62	63
V4	65	62	62	63	61	63	66	62	67	63
V5	86	81	80	79	79	85	76	81	81	77
V6	66	61	59	61	61	62	59	64	58	54
V7	24	28	26	28	19	33	26	22	26	31
V8	47	47	42	44	48	43	43	50	47	43
V9	32	28	33	30	31	31	30	32	30	31
V10	73	67	64	67	69	68	64	72	66	59
V11	37	33	39	33	39	32.5	34	37	35	36
V12	43	43	41	42	42	42	42	43	45	40
V13	37	35	35	34	35	40	31	35	35	34
F1	63	59	61	60	56	59	62	59	56	53
F2	70	69	70	69	68	71	73	67	72	65
F3	49	53	52	50	48	52	54	48	50	45
F4	26	26	26	26	23	25	25	24	24	22
F5	61	60	61	62	57	60	61	59	59	53
F6	25	25	26	26	23	25	25	25	25	23
F7	12	13	12	12	13	14	13.5	12.5	11	10
F8	11	10	13	10	10.5	11	10	10	9.5	9
F9	14	13	14.5	14	12	12	14	13	13	14
F10	33	29	33	31	31	29	35	30	35	32
F11	17	14	17	16	14.5	16	17	15	13	13
F12	18	17	18.5	18	17	17	20	16	16.5	15.5
F13	40	35.5	39	37	37	40	42	37	38	36
F14	10	12	12	10	10	12	11	10	11	10
F15	63	58	59	58	56	60	61	59	61	56
F16	76	73	75	74	69	72	75	71	75	72
F17	39	37.5	37	39	36	38	39	39	39	36
F18	7	4	6	5.5	5.5	6	5	7	4	4
F19	28	28	29	27	26	28	26	27	27	26

Hyl (m)	14.12 8.1	14.12 8.5	14.12 8.3	14.12 8.6	55. 1497	14.12 8.2	14.8. 22.2	55. 1494	24.9. 2.3	24.9. 2.2
M1	20	16	20	21	18	18	19	15	15.5	19
M2	14	11	14	13	13	13	13.5	12	12	13
M3	12	10.5	12	12.5	11	12	13	11.5	11.5	12
M4	5	4	6	5.5	6	5	5	5	5	4
M5	5.5	4	4.5	4	4.5	5	5	4.5	5	5
M6	6.5	7.5	8	7	8	8	6.5	7	5.5	5.5
M7	6	6	6	6	6	6	5	6	4.5	5.5
M8	11	10	11.5	12	10	11	12	10.5	11	10
M9	21	22	21	22	20	21	19	20	20	20.5
M10	6	6	7	7	6	6	6	6	6	5.5
M11	12	11	11.5	12	9	12	10	10	12	11.5
M12	19.5	18	18	19	18.5	19	19	18	19	19
M13	3	3	3.5	3.5	3.5	3	3	3	3	3
M14	4	3.5	3.5	4	3	3	3	3	3	4
M15	7	7	6.5	6	5	6	6	6	5	6
M16	7	7	6.5	7	6	7	6	7	6	7
M17	7	6	6.5	7	5	7	6	6	6	7
M18	4	5	5	4.5	5	4	4	5	4	5
M19	6	6	6	5.5	6	6	6	5.5	6	6
M20	5	5	5	5	5	5	5	5	5	5
M21	7	6	6	6	–	6	6.5	6	5.5	6
M22	6	5.5	5	5	–	5	5	5	5	5
P1	41	39	43	39	39	40	42	40	42	42
P2	35	34	34	35	31	33	32	33	34	30
P3	16	16	18	18	18	17	20	15	19	16
P4	21	21	20.5	23	19	21	20	21	22	19
P5	3	2.5	3	4	3	2.5	5	2	2.5	2.5
P6	6.5	6	7.5	7	6	7	8	6	7	6.5
P7	10	8	10	9	7	6	9	8.5	9	9
P8	9	9	10	9	9.5	8.5	9	9	9	9
P9	9	8.5	10	8.5	9	9	8	9	9	9
P10	18	16	17	17.5	17	17	16	16	17	16.5
P11	4.5	4.5	5	5	5	4	4	5	4	5
P12	4	3	4	4	3.5	3	3	3.5	3.5	3.5
P13	7.5	7	7	7	6	8	7	–	7	7
P14	7	6	7	7	6	8	6	–	6	6
P15	5	5	6	5	5	5	4	5	5	5
P16	5	5.5	5	5	5	5	5	5.5	5	5
P17	6	6	6	6	6	6	5.5	5	6	6
P18	6.5	6	6	6	6	6.5	6	6	6	6
P19	6	5.5	5.5	6	6	5.5	5	5	5.5	5
P20	6	6	6	6	6.5	6	6	5.5	6	5.5

Pon (f)	1963. 173.12	31a	1976. 1430	1948. 7.6.1	LA.4 .86	LA.2 .86	3.0	3.m	1179. c	1976. 1427
B1	110	100	102	100	101	110	108	103	100	112
B2	47	40	47	45	45	44	44	47	43	47
B3	26	25	30	25	26	23	28	27	24	26
B4	45	39	42	39	41	40	41	42	41	40.5
B5	67	62	67	67	68	67	72	69	65	73
B6	28	28	31	25	28	26	27	27	26	27
B7	32	33	32	29	28	34	33	30	29	33
B8	27	22	22	24	24	28	28	24	24	27
B9	20	16	19.5	17.5	19	22	20	20	17	22
B10	39	34	36	34	38	40	39	37	39	37
B11	29	25	36	26	29	35	34	33	32	25
B12	21	20	27	24	24	30	27	27.5	25	25
B13	46	44	47	47	49	50	49	47	46	53
B14	34	32	30	35	32	29	36	33	31	36
B15	75	66	72	68	72	75	76	75	73	69
B16	27	25	27	28	28	27	26	28	23	28
V1	5	7	4	4	6	7	6	4	3	5
V2	67	62	66	61	63	69	64	61	62	64
V3	96	93	96	92	95	95	97	95	95	93
V4	110	102	105	100	104	113	114	106	103	112
V5	122	114	114	118	123	122	118	120	118	123
V6	70	70	60	69	68	69	62	68	73	73
V7	59	-	59	57	65	60	59	55	55	56
V8	66	63	60	61	64	64	64	65	64	62
V9	57	-	47	60	58	60	62	56	54	59
V10	75	74	63	74	72	72	65	72	81	79
V11	66	-	54	71	64	71	71	65	65	68
V12	79	72	64	62	70	76	68	67	67	68
V13	49	48	50	51	52	49	55	49	53	46
F1	91	84	87	87	86	93	89	88	81	93
F2	134	123	124	129	121	123	137	126	121	133
F3	99	95	101	101	95	95	104	95	91	104
F4	47	44	40	45	39	39	40	46	43	43
F5	78	73	78	78	79	80	82	80	75	82
F6	34	33	35	34	35	35	35	35	35	37
F7	12	11	11	10	10	12	14	11	8	11
F8	10	3	10	9	9.5	10	7	9	7.5	13
F9	22	19	20	19	22	19.5	20	21	19	20.5
F10	74	74	100	66	68	77	76	84	75	82
F11	33	32	41	30	32	39	36	33	36	38
F12	43	43	56	41	40	41	45	44	46	47
F13	74	68	82	69	68	69	77	72	71	78
F14	26	27	34	27	23.5	29	33	26	30	29
F15	100	90	89	88	95	99	92	92	90	100
F16	137	130	147	131	145	149	137	142	134	155
F17	79	73	68	74	78	79	77	74	72	84
F18	3	7	5	6	6	5.5	6	5.5	6	6
F19	32	30	32	29	35	32	29	36	28	32

Pon (f)	1963. 173.12	31a	1976. 1430	1948. 7.6.1	LA.4 .86	LA.2 .86	3.0	3.m	1179. c	1976. 1427
M1	48	48	45	44	48	55	49	51	46	55
M2	31	34	32.5	33	28	38	35	31	32	34
M3	31	33	33	32	30	40	35	30.5	34	35
M4	15	11	14	12	9	10	11.5	11	9.5	10
M5	14	15	12	17	16	15	17.5	16.5	14.5	15
M6	16	16	15	17.5	19	18	16	16.5	16	17
M7	13	14	15.5	17	15.5	15	13	15	15	15
M8	27	25	27	25	28	33	28	28	24	25
M9	36	33	34	32	33	32	34	36	32	39
M10	14	13	16	15	15	16	15	15	15	14
M11	20	20	20.5	22	23	22	20	22	21	22
M12	36	38	37	40	37	39	36	36	40	40
M13	–	9	9	9	9	9	8	8	9	7.5
M14	–	9	9	10	8	10.5	9	9.5	9	9
M15	9	10	11	11	11	12	10.5	11	11	10
M16	9	10	11	12	11	14	10	12	12	11
M17	11	12	11	11.5	13	11	11	12	11	12
M18	10	10	10.5	12	9	13	10	11	11	12
M19	12	12	13	12	12	12	12	11	13	12
M20	11	11	11.5	11.5	11	11	11	11	12	12
M21	12	14	13	12	12.5	12	12	12	13	14
M22	10	11	12	11.5	11	11	11	11	12	11
P1	72	69	80	73	77	82	75	78	74	82
P2	60	56	61	57	59	61	60	60	56	58
P3	37	35	35	34	40	42	41	38	33	37
P4	37	33	39	30	34	33	37	36	32	35
P5	10	10	13	10.5	5	13	9	8	11	11
P6	14	11	18	12.5	9	15	12	10.5	14	15
P7	15	14	18	14.5	18	18	16	19	15	23
P8	18	17	21	17	19	21	18	19.5	20	19
P9	15	17	18	18	17	20	17	18	18	18
P10	31	33	34	32	29	31	31	32	34	31
P11	–	13	15	13	14	15	12.5	13	15	12.5
P12	–	11	13	11	11	13	11	11	11	11
P13	12	11	14	13	12	14	13	13	12	13
P14	10	10	10	11	10	12	8	10.5	11	12
P15	8	9	10	9	10	11	9	9.5	10	10
P16	11	11	11.5	12	12	14	11	11.5	12	13
P17	11	11	12	12	11	11	11	11	12	11
P18	12	12	13	12.5	12.5	13	12	12	13	13
P19	11	12	9.5	11	9.5	10.5	10	11	12	11
P20	12	11	12	13	12.5	14	12	12.5	13	12

Pon (m)	1984. 54.11	1963. 173.13	1939. 1019	1948. 10.30.	LA.1. 86	LA.19 86	LA.11 86	56.11 8.2	1868. 4.16.2	3. e.e
B1	115	124	109	110	120	143	123	112	128	117
B2	48	46	51	49	49	47	49	47	52	47
B3	29	28	30	28	24	27	29	26	28	31
B4	40	42	45	41	44	49	48	42	49	47
B5	70	79	58	57	64	72	79	67	80	79
B6	34	42	29	29	41	46	35	31	41	34
B7	35	42	31	32	36	50	38.5	34	40	38
B8	28	28	29	26	31	30.5	27	27	32.5	25
B9	22	24	22	21	24	22	24	19	24	17
B10	40	42	43	44	43	47	51	35	45	38
B11	26	28	32	33	28	29.5	39	33	26	32
B12	26	22	26.5	26.5	26.5	25	32	28	26.5	24
B13	70	62	55	52	48	63	60	49	58	54
B14	46	44	38	38	39	53	46	36	47	38
B15	75	82	82	76	84	80	89	73	82	74
B16	28	33	28	26.5	37	34	36	22	38	27
V1	4	6	3	4	9	5	6	4	6	4
V2	58	61	66	63	70.5	65	72	62	70	69
V3	90	93	101	95	104	94	95	91	100	100
V4	115	129	114	113	123	144	129	111	136	123
V5	121	136	125	121	144	135	134	117	133	124
V6	70	75	59	71	75	74	77	64	79	77
V7	-	-	78	61	65	-	-	61	-	61
V8	-	-	63	57	65	73	79	60	62	65
V9	-	-	53	53	75	-	-	60	-	54
V10	73	80	64	76	81	80	81	68	87	82
V11	-	-	57	60	87	-	-	69	-	62
V12	-	76	70	67	72	75	75	70	69	72
V13	-	54	58	52	61	55	60	45	55	50
F1	106	112	95	82	116	116	104	92	113	102
F2	162	166	133	132	148	175	166	129	158	146
F3	110	132	105	103	113	139	116	100	128	107
F4	51	56	49	45	48	56	50	43	49	51
F5	77	85	79	82	99	101	103	84	98	89
F6	32	36	35	36	43	43	45	37	44	38
F7	12	13	7	11	13	16	13	10	14	12.5
F8	-	6	9	7	12	13	12	9	8	12
F9	26	26	23	21	25	27	28	20	25	22
F10	112	121	106	86	82	124	94	91	119	85
F11	46	52	42	41	43	56	47	43	52	39
F12	68	74	59	56	54	73	57	52	77	55
F13	91	104	80	84	88	104	94	79	114	86
F14	34	48	35	32	34	50	35	32	49	32
F15	106	110	98	92	111	113	106	95	113	104
F16	178	185	161	153	166	208	185	151	195	160
F17	103	97	80	81	82	99	100	79	102	89
F18	2	7	4	5	4	2	-3	6	4	5
F19	37	49	39	35	45	47	32	36	55	38

Pon (m)	1984. 54.11	1963. 173.13	1939. 1019	1948. 10.30.	LA.1. 86	LA.19 86	LA.11 86	56.11 8.2	1868. 4.16.2	3. e.e
M1	76	74	64	55	62	84	68	57	66	54
M2	48	49	37	34	44	59	40.5	37	44	33
M3	45	43	35	35	45	52	38	36	40	33
M4	28	17	14	10	16	16	19	11	16	15
M5	21	21	16	18	17	18.5	19.5	14	21	18.5
M6	24	24	18	18	20	22	18.5	18	21	20
M7	22	18	17	16	15.5	19	16.5	14.5	17	17
M8	29	29	28	22	31	39	35	23	30	25.5
M9	36	40	37	31	35	44	43	34	40	38
M10	16	17	18	15	15	17	17.5	15	18	14
M11	23	27	27	23	26	26	28	25	26	24
M12	44	43	44	41	45	43	45	46	42	40
M13	–	10	10	9	9	9	9.5	10	10.5	9
M14	–	11	11	9.5	10	11	11	10	10.5	9
M15	–	15	14	12	12	14	15	13	12	14
M16	–	18	15	13.5	14	17	17	13.5	14	14
M17	11	14	14	12	14	14	15	14	15	13
M18	12	14	13	12	13	12	10.5	11	12	12
M19	13	15	14	13	13	13.5	13.5	15	14	13
M20	12	13	13	12	13	12.5	12	12.5	13	12
M21	16	15	15	13.5	15	14	16	16	15	13.5
M22	13	13	13	11	13	14	14.5	13	13	11.5
P1	94	95	88	82	92	121	104	81	94	84
P2	67	71	68	59	67	77	73	61	70	66
P3	40	42	38	33	36	50	48	30	41	39
P4	38	41	39	35	40	45	43	32	46	42
P5	14	19	15	12	17	22	24	13	18	7
P6	14	19	16	15	15	18	19	16	26	13
P7	22	20	20	18	21	33	27	16	17	16
P8	21	25	22	20	20	25	24	20	22	19
P9	20	20	20	18	21	20	21	18	19	19
P10	38	39	38	34	37	38	37	37	38	31
P11	–	16	16	15	14	16	15	15	16	13
P12	–	14	14	12	12	14.5	15	11	14	11
P13	–	18	17	15	17	17	20	16	16.5	16
P14	–	19	14	14	13	16	15	13	13	12
P15	11	11	10	10	11	10	12	10.5	11	10
P16	12	14	14	11.5	14	14	15	12	14	10
P17	13	13	13	12	12	13	13	13	14	12
P18	13	14	15	12.5	13	14	14	13.5	13	12
P19	14	15	13	11	13	12.5	14	13.5	14	13
P20	15	15	14	13	14	15	16	14	14.5	12

Gor (f)	4.12. 31	2.7. 79.1	1979. 420	1979. 422	LA.20 86	M.729	FC. 146	M.460	M.878	Z.II. 63
B1	129	120	122	116	128	120	106	112	122	115
B2	52	38	46	44	52	50	43	50	50	45
B3	29	23	27	22	25	27	26	23	22	27
B4	50	49	50	48	51	48	43	47	43	49
B5	69	72	80	71	75	78	67	62	61	69
B6	35	34	31	35	36	34	33	37	35	32
B7	41	44	41	36	41	36	33	32	37	36
B8	29	27	28	28	30	28	28	29	32	27
B9	27	29	28	27	30	27	27	27	26	26
B10	43	50	46	45	50	46	45	46	46	45
B11	30	29	29	29	33	37	30	33	32	32
B12	28	27	28	26	30.5	33.5	27	28.5	30	27.5
B13	59	52	53	57	64	60	56	55	54	52
B14	39	37	38	35	43	35	37	37	39	33
B15	78	79	77	78	87	85	79	82	84	79
B16	30	19	29	25	31	29	32	31	29	25
V1	4	3	3	4	8	3.5	3	5	3	1
V2	69	66	62	70	70.5	70	68	70	73	63
V3	100	90	94	102	102	101	100	101	100	94
V4	120	113	117	118	128	120	111	116	121	116
V5	155	148	151	160	169	164	154	152	155	133
V6	79	74	78	84	89	82	84	84	81	74
V7	71	69	75	76	75	78	72	66	71	55
V8	60	57	57	69	63	66	65	64	62	54
V9	62	62	69	58	90	63	59	67	64	56
V10	85	82	91	90	105	92	90	96	96	82
V11	75	70	72	68	106	76	70	78	78	68
V12	65	64	65	78	80	67	70	73	68	64
V13	66	62	65	67	66	65	65	60	68	51
F1	115	109	112	113	120	116	112	113	116	101
F2	148	142	150	143	149	137	128	142	140	130
F3	116	112	108	105	110	106	95	107	106	100
F4	61	56	62	54	61	51	54	52	48	52
F5	99	95	103	97	113	107	104	100	106	91
F6	38	40	42	40	48	43	45	42	43	40
F7	24	19	16	19	17	21	17	15	18	18
F8	22	22	26	25	24	17	22	23	20	18
F9	31	29	33	30	35	28	28	26	27	29
F10	117	102	109	102	96	95	100	101	93	111
F11	46	48	47	37	44	42	42	44	43	44
F12	67	65	68	55	59	58	57	65	61	67
F13	100	99	101	95	86	92	94	93	91	92
F14	41	45	40	37	32	38	36	40	39	38
F15	120	118	120	120	129	123	114	118	115	108
F16	172	161	168	160	187	167	161	163	162	165
F17	97	86	93	90	97	94	87	90	89	84
F18	12	13	8	11	12	13.5	16	9	5	10.5
F19	63	64	64	57	54	46	50	45	42	53

Gor (f)	4.12. 31	2.7. 79.1	1979. 420	1979. 422	LA.20 86	M.729	FC. 146	M.460	M.878	Z.II. 63
M1	50	42	51	49	61	52	50	51	49	52
M2	34	33	35	33	36	30	31	31	33.5	33
M3	36	31	38	33	37	35	33	34	34	33
M4	16	12	18	11	15	15	13.5	13	16	14
M5	15	18	20	20	24	14.5	18	16	18	16
M6	23	21	24	20	27	20	22	21	21	19.5
M7	18	16	20	16	20	17	18	18	17	15
M8	23	23	25	28	33	28	25	27	24	23
M9	33	32	32	31	37	30	33	35	34	32
M10	14	12	14	12	15	13.5	14	14	14	14
M11	23	20	21	22	26	25	24	25	25	23
M12	45	44	47	48	53	47	47	48	47	47
M13	8	7	8	–	8	7	7	8	8	8
M14	8	6	8	–	9	8	8	8	7.5	8
M15	10	8	11	–	11	13	12	12	12	13
M16	13	10	11	–	13	13	12	13	12.5	12.5
M17	13	11	12	13	15	14	13	13	13	14
M18	11	10	12	11	13	12.5	12	14	13	11
M19	14	14	14	15	17	15	16	16	14	14.5
M20	13	11	12	12	15	13	14	13	13	12
M21	15	14	16	15	20	16	17	17	16	15
M22	13	12	14	14	17	14	13.5	13.5	14	13
P1	91	82	85	80	107	92	91	89	88	91
P2	64	64	66	62	75	64	62	64	62	64
P3	34	35	40	33	47	37	35	38	37	35
P4	32	39	38	33	38	33.5	32	34.5	32	33
P5	11	11	10	7	10	10	8	13	10	12
P6	17	20	12	9	13	16	16	18.5	18	17
P7	21	13	15	15	23	20	18	15	18	18
P8	20	16	20	19	22	20	19	19	20	21
P9	21	18	19	20	22	22	20	21	21	20
P10	39	38	42	42	47	43	44	40	40	41
P11	13	13	11	12	13	13.5	13	13	13	14
P12	10	8	9	9	10	10	9.5	10	9.5	9.5
P13	14	13	13	14	15	15.5	15	15.5	15	15
P14	12	10	11	9	11.5	12.5	12	12	11	13
P15	11	10	10	10	12	11	10	11	11	10
P16	14	12	14	13	16.5	15	15	14	14	14
P17	14	14	14	14	16	15	15	15	14	14
P18	15	13	14	15	17	14.5	15	14.5	14	14
P19	13	14	15	13	17	14	14	14	13	13
P20	14	13	14	14	16.5	15	13.5	14	13	14

Gor	1984.	1963.	1984.	48.	48.	M.717	FC.	M.505	FRC.	M.342
(m)	54.3	173.15	54.2	436	435		115		133	
B1	144	135	156	135	135	124	110	127	120	135
B2	50	48	57	55	50	53	44	56	53	50
B3	32	30	34	33	31	28	28	29	34	29
B4	58	56	57	49	49	48	46	52	53	50
B5	78	88	90	76	74	63	63	78	73	75
B6	49	39	46	39	40	41	36	36	35	41
B7	50	45	51	41	44	36	35	36	34	45
B8	33	36	30	27	29	30	25	27	25	27
B9	32	37	28	27	29	27	26	22	25	26
B10	49	52	47	47	50	47	43	44	46	50
B11	34	30	34	37	34	36	33	36	34	36
B12	29	27	33	36	32	31.5	29	32	30	30
B13	71	70	65	72	62	58	63	61	61	68
B14	45	48	51	53	50	39	34	36	34	40
B15	91	84	91	90	92	87	79	83	85	89
B16	38	30	36	35	37	28	25	27	28	32
V1	5	5	3	4	3	2	3	3	3	3
V2	72	73	70	75	68	67	67	72	77	71
V3	104	102	107	100	96	100	99	105	100	101
V4	144	134	150	145	142	125	114	125	124	133
V5	175	175	172	160	173	152	147	154	155	165
V6	–	–	–	–	–	84	75	84	94	80
V7	–	–	–	–	–	64	56	59	60	74
V8	–	–	–	–	–	66	61	65	63	60
V9	–	–	–	–	–	63	64	69	60	64
V10	–	–	–	–	–	94	82	92	102	87
V11	–	–	–	–	–	74	82	85	77	–
V12	–	–	–	71	73	77	70	73	75	79
V13	–	–	–	60	68	56	59	58	61	67
F1	141	136	148	134	116	112	99	112	120	121
F2	177	176	188	176	167	146	134	144	150	152
F3	126	134	132	131	128	109	104	108	101	113
F4	68	74	69	70	65	58	59	62	51	53
F5	121	120	125	122	116	100	100	105	106	106
F6	47	48	49	50	45	41	41	44	45	44
F7	32	27	31	28	30	20	19	23	19	21
F8	26	27	24	23	22	19	21	27	24	24
F9	34	36	39	39	34	29	28	29	27	28
F10	130	136	135	111	110	120	116	105	116	121
F11	58	53	59	46	54	51	46	41	47	51
F12	85	74	83	67	75	75	65	65	68	76
F13	123	115	128	108	108	103	91	95	102	106
F14	46	43	47	47	50	43	36	38	44	42
F15	141	140	153	137	132	125	114	121	121	127
F16	200	203	207	195	194	181	174	173	172	192
F17	110	112	111	113	106	92	92	93	94	103
F18	14	10	15	11	14	13	9.5	13	11	10
F19	73	79	82	48	60	56	51	52	49	57

Gor (m)	1984. 54.3	1963. 173.15	1984. 54.2	48. 436	48. 435	M.717	FC. 115	M.505	FRC. 133	M.342
M1	63	57	65	62	66	57	52	55	49	67
M2	42	37	41	37	39	36	37	31	31	44
M3	38	40	41	34	39	34	36	35	32	37
M4	20	19	20	18	18	17	16	22	15	17.5
M5	24	17	24	30	21	20	23	18	16	26
M6	24	27	27	26	27	25	25	26.5	23	25
M7	16	20	17	18	19	16	18	18	18	18.5
M8	24	25	27	23	25	23	21	23	23	25
M9	39	35	36	35	37	33	33	31	35	38
M10	14	15	15	13	13	14.5	13	13	13	14
M11	26	26	29	26	23	25	23	25	23	25
M12	52	51	53	47	47	50	48	49	44	50
M13	8	–	–	8	–	7.5	8	7	8	8
M14	9	–	–	8	–	8	9	9.5	9.5	9
M15	14	13	17	16	14	15	13	16	14	13
M16	18	16	23	18	16.5	16	14.5	18	15	17
M17	16	15	19	16	13	15	13	15	13	14
M18	15	12	12	14	13	15	13	15	13	14
M19	15	16	16	16	15	15	15	15.5	14	16
M20	13	13	14	13	13	13	13	13	13	14
M21	17	17	18	17	16	17	16	17	15	17
M22	15	15	16	14	15	13	13	15	13.5	15
P1	98	107	112	103	107	101	95	93	92	103
P2	72	71	76	68	66	62	64	64	69	74
P3	37	40	41	35	37	35	34	33	33	40
P4	41	40	42	40	36	35	33	32	39	42
P5	10	8	12	9	8	10	8	7	10	13
P6	19	16	23	18	16	17	17	13	19	20
P7	17	20	19	20	22	20	17	18	18.5	16
P8	20	22	23	20	20	20	19	20	19	18
P9	22	22	22	21	21	20	19	21	19	20
P10	43	46	46	40	41	41	42	42	40	44
P11	13	10	–	14	–	14	13	13	13	13
P12	10	9	–	10.5	–	10.5	11	10	11	10
P13	21	19	26	22	18	20.5	18	21	17	19
P14	17	15	20	16	16	16	15	18	14	16
P15	12	12	12	10	11	11	11	11	10	11
P16	15	17	17	15	15	15	14	15	15	15
P17	14	16	15	15	15	14	14	15	13	15
P18	14	15	16	14	14	14.5	15.5	15	14	15
P19	15	16	17	15	14	14.5	14	16	13	13
P20	14	15	17	13	15	14	14	15	13	15

Pan (f)	64.12 .1.7	1939 .3369	20.4 .13.2	1939 .3382	LA.6 .86	LA.8 .86	TW.13 .84	1982 .546	1939 .3378	1939 .992
B1	95	102	104	103	108	107	106	110	97	97
B2	40	43	42	42	39.5	36	40	48	38	41
B3	23	26	23	26	20.5	20	24	27	20	20
B4	41	40	43	44	40	40	43	47	40	38
B5	63	62	61	64	63.5	67	60	64	60	60
B6	24	25	26	27	26	24	25	28	26	25
B7	30	30	33	33	36	37	34	31.5	30	29
B8	24	23	22	25	26	20	21	27	22.5	24
B9	20	23	21	21	24	20	21	26	18	23
B10	40	38	39	42	45	38	37	45	38	38
B11	25	28	30	27	25.5	29	28	33	28	27
B12	23	25	28.5	21	21	21	22	26	21	21
B13	44	47	47	52	51	47	50	53	49	47
B14	29	32	28	30	28.5	23	28	31	30	28
B15	68	71	72	70	75	75	71	83	67	67
B16	27	26.5	26	24	26	27	27	30	25.5	23
V1	2	2	3	3	5	7	5	3	3	3
V2	72	67	66.5	77	74	69	67	72	74	68
V3	98	98	99	95	94	93	92	104	96	95
V4	105	108	108	105	109	105	107	115	104	104
V5	133	126	122	131	144	134	131	144	130	131
V6	67	74	65	71	80	71	73	81	72	75
V7	69	58	54	63	59	60	57	67	65	67
V8	59	61	59	65	70	61	61	62	61	–
V9	53	52	54	51	58.5	56.5	53	50	50	49
V10	75	80	70	79	96	78	81	91	80	88
V11	63	59	64	58	76	67.5	65	60	59	60
V12	65	64	58	64	66	67	61	66	65	67
V13	55	53	55	45	56	55	59	57	53	55
F1	104	95	92	112	104	96	102	102	104	105
F2	114	123	112	121	118	105	111	122	113	113
F3	88	83	83	91	85	76	81	91	88	84
F4	55	54	46	54	52	46	50	55	52	51
F5	94	97	85	103	97	86	93	97	93	95
F6	40	38	38	40	41	36	38	42	40	37
F7	20	22	12	22	19	18	16.5	17	15.5	20
F8	14.5	14	13	14	9.5	12	11	15	12	11
F9	22	29	22.5	27	25	27	26	24	23	24
F10	75	86	82	90	89	84	92	78	72	77
F11	32	36	38	34	42	38.5	41	40	30	34
F12	46	50	49	52	54	49	57	51	42	50
F13	66	70	66	76	82	66	72	78	64	68
F14	26	28	29.5	32	27.5	23	32	31	28	24
F15	98	96	93	104	111	104	97	109	100	99
F16	132	136	132	152	149	147	146	144	131	130
F17	73	74	74	81	76	75	74	82	75	72
F18	9	8.5	5	12.5	6	7	5	14	8	6
F19	31	32	28	32	36	37	33	33	25	27

Pan (f)	64.12 .1.7	1939 .3369	20.4 .13.2	1939 .3382	LA.6 .86	LA.8 .86	TW.13 .84	1982 .546	1939 .3378	1939 .992
M1	42	39	39	45	47.5	47	49	45	35	38
M2	25.5	26	24	29	31	28	31	30.5	25	29
M3	25.5	26	23.5	28.5	27.5	26	28	26	25.5	29
M4	10.5	10	6	13	9	8	8.5	6	8	8
M5	12	12	13	16.5	13	12.5	12	15	14.5	11
M6	17.5	15	16	15	15	18	18.5	16	15	18
M7	14	13	15	14	12.5	15	15	13	14.5	14.5
M8	25	22	27	31	28	28	28	29.5	25	26
M9	34	35	35	39	39.5	38.5	35	38	34	34
M10	15	13.5	14	13.5	13.5	15	15	15	15	15
M11	17	18	16	17	18	20	18	16.5	18	18
M12	33	34	33	32	33	33	34	35	33	32
M13	8.5	8	8	7	7.5	10	8.5	8	–	8
M14	9	9	8.5	7.5	8	9	9	8.5	–	8.5
M15	9	13	10	10	10	9.5	12	12	9	10
M16	10	14	10.5	10	11	11	12	13	11	10
M17	10	10	9	10	10.5	11	11	10	10	10
M18	9	10	8	9	7.5	9	10	10	9	9
M19	11	11	11	11	10.5	11.5	10.5	12	11	10
M20	9	10	10	9	9.5	10.5	10	10	10	9.5
M21	11	11.5	11	10	11	10.5	12	10.5	11.5	10.5
M22	10	10	10	9.5	11	10	11.5	10	11.5	10
P1	67	68	70	80	78	81	76	75	68	66
P2	55	56	56	59	60.5	61	62	62	55	56
P3	33	32	34	41	41	40	39.5	40	37	36
P4	32	35	34	37	39	38.5	37	38	33	32
P5	5.5	6.5	5.5	6	8.5	7	7	12	5.5	8
P6	13	12.5	13	14	14	13	13	13.5	10	15
P7	13	12.5	15	21	15	21	18	16	14	17
P8	18	18	18	18	18	20	20	19.5	18	19
P9	14.5	15	14	13	14	16	14	15	14.5	14
P10	31	30	30	28	27	29	30	31	30	27
P11	12.5	12	11	11	11	13	12	13	11	11
P12	10	9.5	9	9	9.5	10.5	10	9	9	8
P13	11	15	11	11	10	12	13	11	11	10
P14	9	12.5	9	9	11	9	10	8.5	9	8.5
P15	8	8.5	8	9	7.5	9	8	8	8	8
P16	10	11	10	9	10	11	11	11	10.5	9.5
P17	11	10	11	10	10	11	11	11.5	10.5	9
P18	11.5	12	11	11	11	12	11	12	12	11
P19	10.5	10	9	10	10	9	10	9.5	9	8.5
P20	11	11	11	11	11.5	11	12	10.5	12	9

Pan (m)	1939 .3363	1939 .951	1939 .3365	50 .1863	1939 .3364	24.8 .6.1	1922.1 .19.1	1.8. 9.10	76 .1797	2.a
B1	111	108	107	110	103	104	113	98	111	104
B2	43	42	43	42	42	46	47	40	42	42
B3	23	24	24	24	26	22	27	25	25	23
B4	44	44	43	45	41	42	42	42	50	43
B5	62	69	68	60	66	60	75	59	68	71
B6	27	28	27	23	28	27	28	26	30	27.5
B7	36	35	35	35	31	30	35	30	37	33
B8	26	23	25	22	27	24	26	23	22	21
B9	23	23	23	21	26	19	20	19	22	21
B10	40	38	40	41	40	33	39	37	42	37
B11	28.5	26.5	27	30	33	32	34	29.5	29	26
B12	24	22.5	22	23	23	25	27	25	24	23
B13	53	52	53	54	51	49	55	53	53	50
B14	35	34	33	34	32	35	36	30	35	36
B15	69	64	66	75	73	76	78	72	76	72
B16	29	28	29	27	25	25	28	28	30	27
V1	3.5	3	3	4	2	3	2	2	2	3
V2	72	74	70	73	66	71	71	69	70	66
V3	97	105	94	108	94	101	102	97	96	97
V4	117	111	108	112	105	110	115	104	113	110
V5	136	139	133	139	125	130	136	134	132	136
V6	75	80	74	78	68	72	81	75	71	78
V7	64	64	68	69	56	69	69	65	68	65
V8	59	67	57	64	57	59	63	66	59	63
V9	57	58	53	55	50	47	51	51	51	48
V10	82	87	83	84	77	79	92	88	85	94
V11	67	69	59	64	58	57	57	60	55	56
V12	66	68	58	72	58	64	66	67	67	64
V13	52	59	49	58	50	60	51	55	44	51
F1	111	109	101	107	102	102	113	105	103	100
F2	128	130	127	125	120	127	130	116	138	128
F3	91	91	90	85	89	84	92	90	98	87
F4	57	57	52	55	53	50	57	58	61	54
F5	105	100	94	100	95	93	103	98	102	91
F6	43	42	40	39	39	38	43	39	42	38
F7	20	20	17	19	17	22	19	22	22	19
F8	13	16	10	6	13	9	11	9.5	13	–
F9	27	24.5	24	25	25	25	28	26	27	29
F10	94	78	81	80	89	84	90	79	99	88
F11	44	34	36	34	39	36	40	32	43	36
F12	59	49	51	51	50	48	56	44	62	52
F13	78	76	71	78	69	72	75	67	88	77
F14	34	28	33	29	32	27	28	30	34	28
F15	111	104	107	107	97	100	110	106	112	109
F16	155	142	145	141	142	140	153	143	158	150
F17	85	77	80	79	78	77	86	79	85	76
F18	10	10	8	9	5.5	6.5	12	13	9	11
F19	31	33	30	30	33	29	38	34	36	33

Pan (m)	1939 .3363	1939 .951	1939 .3365	50 .1863	1939 .3364	24.8 .6.1	1922.1 .19.1	1.8. 9.10	76 .1797	2.a
M1	46	42	44	44	45	43	47	39	49	48
M2	30	28	27	26.5	27	27	31	25	33	30
M3	30	28	26	26	26	25	30	30	31	31
M4	9	8.5	9	8.5	8	8	10	8	8	10
M5	14	13.5	14	13	12	14	14	14	14	13
M6	19	17	15.5	18	14.5	14	18	15	18	19
M7	16	15	14.5	16	14	12	15	13.5	14.5	15
M8	23	25	23	27	25	22	27	27	31	30
M9	35	37	37	36	35	32	35	34	42	37
M10	14	17	13	15	13	14	15	15	17	17
M11	17	16	16	17.5	10	17	19	15	18	17
M12	32	37	34	32	32	31	36	33	36	33
M13	–	8	8	7.5	7	8	7.5	7	–	8
M14	–	10	9	9	9	8	9	8	–	9
M15	11	12	13	11.5	11	10	12	12	14	14
M16	12	14.5	14	13.5	14	12	13	12.5	15	13
M17	10	9	10	9	11	9	11	8	12	9
M18	9	11.5	11	9	8	10	10	9	10	9.5
M19	10	12	10	11	10	10.5	12	11	12	12
M20	9.5	11	10	10	10	10	11	10	11	10.5
M21	10	13	11.5	10	10	9	12	11	11	10
M22	10.5	11	10.5	10	10	9	12	10.5	10.5	10
P1	74	72	70	70	72	70	79	79	79	76
P2	61	62	58	57	58	55	59	54	63	62
P3	39	39	32	35	35	33	36	37.5	38	40
P4	38	36	36	35	34	32	37	33	40	38
P5	10	8	5	8	9	6	9	3	9	10
P6	17	16	13	14	16	12	17	12	15	16
P7	18	17	14	13	15	15	15	21	17	21
P8	18	20	18	19	18	18	19	19	19	21
P9	15	16	14.5	14	13	15	16	14	17	16
P10	30	31	30	29.5	28	27	34	29	31	30
P11	12	13.5	12	12	11	11	11	11	–	13
P12	8	10	9	10	9	10	9	9	–	10
P13	13	14.5	14	14.5	15	12	15	14	15	12
P14	12	13.5	13	11	12	13	13	14.5	13	14
P15	7.5	8	8.5	8	7	9	8	7	9.5	10
P16	10	11	10.5	10.5	11	11	13	10	11	10.5
P17	10	11	11	10	10	10	12	11	11.5	11
P18	11	12	11.5	11.5	11	11	12		11.5	12
P19	9.5	12	9.5	9	9	9	12	10	10.5	10
P20	11	12	12	10.5	11	10	13	11	11	11

Hom (f)	A3272	A2307	A3059	A2764	A2890	A2848	A2849	A3124	A3291	A2213
B1	100	105	94	109	108	98	95	98	105	101
B2	55	63	52	63	64	55	54	59	55	59
B3	30	35	32	36	40	31	31	32	34	34
B4	50	55	50	56	59	45	48	49	57	52
B5	70	80	80	88	85	79	77	80	76	79
B6	27	30	26	24	25	25	24	22	24	25
B7	22	21	21	23	21	22	21	19	26	21
B8	20	22	18	21	18	21	18	19	20	20
B9	16	19	14	18	17	18	15	17	15	18
B10	33	38	33	36	35	37	31	32	33	33
B11	34	38	32	34	37	37	36	38	36	38
B12	27	30	26	27	29	30	29	29	28	29
B13	41	50	46	46	48	46	40	48	44	43
B14	26	29	30	29	32	30	25	28	27	28
B15	73	82	70	73	81	75	71	73	74	76
B16	22	23	22	25	28	21	22	22	23	25
V1	6	9	7	10	7	7	8	5	6	6
V2	87	103	100	107	99	95	94	89	93	97
V3	128	138	135	131	136	125	123	132	137	140
V4	108	118	107	117	119	107	103	111	116	112
V5	178	192	175	186	196	182	182	185	175	180
V6	105	120	108	109	118	105	113	112	103	111
V7	112	121	114	119	114	108	110	117	107	102
V8	89	96	90	92	98	89	92	97	89	94
V9	93	93	92	95	102	99	98	99	99	102
V10	121	137	121	127	135	121	130	127	116	132
V11	114	102	112	114	125	118	120	120	123	120
V12	110	117	111	119	111	107	107	115	109	110
V13	95	94	97	91	108	95	99	98	95	99
F1	101	118	104	115	112	103	104	102	104	104
F2	121	125	121	131	133	119	118	117	123	117
F3	95	99	87	96	97	88	88	91	90	91
F4	54	65	48	63	63	51	56	53	56	53
F5	95	111	99	107	109	97	99	95	98	100
F6	40	45	42	44	45	42	42	39	40	42
F7	19	27	21	27	25	19	20	20	22	21
F8	17	13	18	18	14	14	15	13	14	15
F9	26	28	26	28	27	24	27	27	30	29
F10	63	72	64	73	69	64	62	68	64	66
F11	30	35	29	28	29	35	32	31	27	31
F12	39	44	35	41	40	40	39	37	35	38
F13	60	69	62	67	65	65	62	62	61	64
F14	27	25	22	21	23	29	22	25	23	23
F15	105	118	102	120	114	110	103	110	106	108
F16	112	125	113	126	121	112	110	121	116	115
F17	63	79	70	71	72	73	68	73	67	69
F18	14	16	12	23	18	15	14	13	13	14
F19	25	23	22	31	23	20	20	21	25	21

Hom (f)	A3272	A2307	A3059	A2764	A2890	A2848	A2849	A3124	A3291	A2213
M1	32	33	32	36	35	26	30	38	33	31
M2	27	32	27	32	28	25.5	25	30	28	27
M3	24	27.5	25.5	29	25	22	23	23	25	21
M4	13	18	16	12	18	14	16	14	15	13
M5	13	16	12.5	15	14	11	13.5	14	13	12
M6	14.5	17	13	16	14	12	15	13	13	12
M7	13	16	13.5	15	13	10	13.5	12	13	11
M8	16	15	19	18	15	15	19	19	19	17
M9	37	41	44	49	44	46	45	44	39	44
M10	9	8	10	10.5	8	8	10	10	11	10
M11	14	12	14	14	14	13	14	14	14	13
M12	36	33	32	32	35	32	33	33	34	32
M13	5.5	4.5	5.5	5	5	4.5	5	5.5	5	5
M14	6	5.5	6	5.5	5	5.5	5.5	5.5	6.5	6
M15	7	6.5	7	7.5	7	6	6	7	7	7
M16	8	7.5	8	7.5	8	7	6.5	8	8	7
M17	7	6.5	7.5	7	7	7	7	7.5	7	7
M18	9	9	7.5	8	8	8	7	8.5	9	8
M19	12	11	11	12	11	11	11	11	11	11
M20	11	11	10	10	11	10	10	10	11	10
M21	11.5	11	10	10	11.5	10	11	10	11	10
M22	11	11	10	9	10.5	10	11	10	10.5	10
P1	50	59	51	58	55	49	50	59	57	55
P2	56	67	61	66	61	61	61	59	58	59
P3	22	25	25	27	23	21	24	25	20	23
P4	36	40	40	44	39	41	40	38	35	39
P5	11.5	10	9	5	8	9	6	9	7	8
P6	13	9.5	11.5	10	11	13	14	14	11	12
P7	7	8	8	9	9	7	6	11	9	8
P8	13	15	14	15	13	13	13	15	14	13
P9	13	14	13	15	12.5	13	12	14	14	14
P10	27	31	25	27	27	28	28	27	30	27
P11	9	8	9	9	8	8	8	9	9	9
P12	7	7	7.5	7	7	7	7	7	8	7
P13	8	7.5	8	8	7.5	7	7	7.5	7.5	7.5
P14	9	8.5	8	8	8.5	8	7.5	8	9	8
P15	7	7	7	8	7	7	7	7.5	7	7
P16	10	10	9	9	10	9	8	10	10	9
P17	11	10.5	10	10.5	11	11	10	11	10	11
P18	12	12.5	10.5	11	11	11	10.5	11.5	11.5	11
P19	9	10	8	8	9	8.5	9	9.5	10.5	8.5
P20	12	12	10.5	10.5	11	10	11	11	12.5	10

Hom (m)	A3277	A3279	A3315	A3286	A3287	A3072	A2966	A2921	A3115	A3028
B1	104	108	102	102	94	103	107	96	110	103
B2	63	66	57	61	54	61	56	51	59	59
B3	36	33	31	34	30	35	32	30	34	34
B4	57	50	53	52	49	53	53	48	55	52
B5	83	83	81	81	77	82	83	74	83	83
B6	27	29	29	26	23	24	28	23	22	25
B7	20	21	22	21	20	21	27	23	26	22
B8	21	27	22	20	22	20	22	19	23	23
B9	17	24	19	18	20	17	19	17	18	19
B10	33	38	32	31	36	32	34	33	35	32
B11	40	35	37	40	38	36	37	36	39	37
B12	30	30	27	33	31	29	29	27	30	31
B13	46	49	47	47	51	43	45	44	49	48
B14	26	31	29	29	24	27	27	27	29	31
B15	75	76	74	73	77	71	78	75	77	70
B16	24	25	24	23	22	19	27	22	26	25
V1	5	10	10	8	5	6	7	6	8	5
V2	92	110	102	99	94	97	100	89	104	97
V3	129	143	131	138	133	130	140	122	139	126
V4	112	120	113	115	112	113	116	105	119	115
V5	186	196	190	190	193	186	205	184	188	192
V6	118	118	115	120	123	119	122	110	114	114
V7	111	127	113	116	116	113	115	116	105	121
V8	98	100	94	98	96	93	103	90	90	93
V9	96	103	95	95	93	103	111	90	96	100
V10	137	138	131	140	143	142	143	132	131	130
V11	115	123	116	111	111	124	137	106	117	113
V12	107	119	109	114	110	120	119	110	114	116
V13	98	103	95	103	95	96	111	89	94	97
F1	104	118	114	106	104	107	113	98	111	109
F2	124	127	131	128	120	126	126	115	131	130
F3	87	91	101	96	90	94	94	90	96	93
F4	48	58	68	57	59	55	60	57	60	68
F5	96	108	104	101	98	100	104	95	110	103
F6	40	43	41	43	41	40	43	40	47	43
F7	20	30	27	20	23	24	23	20	23	24
F8	16	20	18	17	17	18	17	18	18	18
F9	23	28	31	28	26	29	30	28	28	28
F10	69	74	72	68	76	73	70	62	59	71
F11	29	31	30	34	37	37	35	27	28	32
F12	36	43	39	40	47	42	43	36	35	40
F13	59	67	67	66	73	66	69	59	64	65
F14	24	25	22	25	27	24	22	24	22	23
F15	113	122	118	113	120	111	120	116	120	117
F16	116	123	125	121	128	119	125	110	122	121
F17	72	78	73	73	76	71	72	69	76	75
F18	20	18	18	15	21	17	17	17	19	20
F19	24	25	28	25	27	27	28	21	26	28