The significance of early hominid cranial variability

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THE SIGNIFICANCE OF EARLY HOMINID CRANIAL VARIABILITY

BY

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ABSTRACT

The aims of this thesis are:

1. To examine patterns of morphological variation in the crania of extant species (*Pan*, *Gorilla*, *Pongo*, and *H. sapiens*) to determine if any common pattern of primate sexual dimorphism exists which could be used in the assessment of fossil hominid sexual dimorphism;
2. To examine patterns of between species variability among the crania of the above extant species to determine if characters exist which could be useful as taxonomic indicators, especially of specific distinctiveness in fossil Hominidae; and
3. To assess the validity of using traits which are dimorphic and/ or variable within species as taxonomic indicators in systematic analyses.

This thesis entails an analysis of inter- and intra-specific diversity among the early hominids based on models derived from samples of modern *H. sapiens* and pongids. Metrical cranial characters were surveyed in order to assess the implications of their variability within the available early hominid sample (*A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, *H. habilis*, and *H. erectus*) using univariate, multivariate, and cladistic analytical techniques.

The univariate analysis found no common pattern of primate sexual dimorphism but it did identify characters of low sexual dimorphism and low variability common to all the extant hominoids. These were used to test the homogeneity of the fossil groups and indicated the possible heterogeneity of *H. erectus*, *H. habilis*, *A. afarensis*, and *A. boisei*. The remaining characters revealed an apparent trend among the hominids (fossil and modern) of dimorphic regions of the skull including the areas of nuchal and temporal muscle attachment, kyphosis of the basicrania, width of the palate, mandible, and base, and facial prognathism.

The multivariate analyses used the patterns of variability and dimorphism known from the modern comparators to assess sex, degrees of sexual dimorphism, and homogeneity of the fossil samples. These analyses revealed the possible heterogeneity of *H. erectus* and *A. afarensis*, the sex of some individual specimens, and some interesting contrasts in the patterns of sexual dimorphism between the fossil and modern species. They also isolated KNM-ER 1805 as having unique basicranial proportions.

Two different types of characters were used in cladistic analyses to determine which type produced the most parsimonious trees and the implications of their use for future cladistic analyses. The results show that non-variable, non-dimorphic traits generally produce more parsimonious trees than variable, dimorphic ones, thus demonstrating the importance of assessing within- and between-group variability of characters prior to cladistic analyses. The method of coding the data prior to the cladistic analysis was tested for its objectivity. The analyses showed that the constant used to code the data into discrete character states had a substantial effect upon the resultant trees.

This study has demonstrated that characters have different properties due to the amount they vary or are dimorphic within groups and that utilising these characters for different purposes has the potential to enhance future systematic/ phyletic studies.

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CHAPTER 1: INTRODUCTION

1.1 Introduction to the Present Study

During the 19th and early 20th centuries, living species were classified on the basis of morphological similarities and differences where a member of a species was envisioned as an 'ideal' type. This method of classification was later replaced by a biological definition (Mayr 1950, 1963) which required groups to be reproductively isolated from sympatric neighbours. But this latter method is difficult to apply to fossil species. Species are composed of populations that are distributed in space and time and which possess similar morphological, physiological, and ecological characteristics (Mayr, 1963). It is populations, not individuals that must be classified, but since populations are not fossilised one can only make inferences from the statistical sample (the individual(s)) to the population (Simpson, 1961). Fossil species are described on the basis of relatively few specimens and are classified using morphological data. The problem of classification is compounded by the fact that species exist and vary in time and space, and, until recently, the lack of knowledge of the extent of this variation within different species.

Variation is always present among species with no two individuals being exactly alike. Some of this variation results from environmental influences during growth and development and some from genetic changes which provide the 'raw material' for long-term evolution. Major changes over long periods of time (ie. speciation) depend on variation and are responsible both for the divergence of populations and increased diversity within a population. Thus the mechanisms of evolution both produce and operate on variation.

Methods of classifying fossils have seen some changes over time within paleoanthropology. From the time of Linnaeus, there has been a well known, well documented tendency for new fossil hominid specimens to be assigned distinct specific or generic names where small differences in shape were taken to indicate differences in 'type' rather than normal within-group variability. Part of the problem, at least initially, was the lack of adequate samples for comparison but the application of the biological species concept helped to reduce the number of species due to an increased appreciation of intra-specific variability. Paleoanthropologists grasped this new way of thinking whole-heartedly, their resistance to further change shown in the reluctance and vehemence with which many greeted such new species names as *H. habilis* and

A. afarensis.

Recently, there has been an indication of acceptance of greater diversity within the hominid fossil record and the importance of within-group variability in determining species limits (eg. Tattersall 1986; Dean 1986; Clarke 1988; Kimbel and White 1988; Grine 1988a). One influential paper is that written by Tattersall (1986) who points out that in closely related species one can expect a large or total overlap in morphological characters so where distinct morphs are readily identifiable they should be assigned to different species unless there is evidence to suggest otherwise. This way of thinking has been taken up by Kimbel and White (1988), for example, to demonstrate the lack of homogeneity in *A. africanus.* This hypothesis, however, does not recognise that differences in morphology may not indicate reproductive isolation (Mayr 1963; Vrba 1980). In successive strata, differences in characters may not indicate species or even sub-species differences, but samples of clines have which replaced each other due to climatic or other changes in environment. This is possible since sympatric populations of a species can differ from one another in a number of characteristics.

The greatly expanded fossil record indicates hominid evolution to have been complex, with multiple taxa usually recognised. However, there is no firm agreement as to the number of species represented, nor of their parameters, and the interpretation of the systematic and phyletic interrelationships of the hominids and their relationship to modern man depends critically upon determination of the number of species represented. In order to recognise distinct species, the amount of variation within a population must first be assessed. Members of any group will vary to some extent with respect to every feature of every bone but variability occurs within the limits of biologically possible phenotypes of that species. Isolated fossils must be assessed in terms of the probable degree of variation within a population and this can only be done in comparison to known, living, organisms, since only a fraction of past populations survive in the fossil record. Thus biological variation in living groups must act as a yardstick with which to measure variability in past populations.

1.2 Biological Variation

1.2.1 Intra-specific Variation

Knowledge of within-group variation is important in any work which tries to group individual fossils together, but people have different expectations about the extent and significance of this type of variation. Some of the kinds of within-group variation include: individual variation, sexual dimorphism, and geographical variation, and change over time, the causes of such variation being both genetic and environmental. Other kinds of variation within the fossil record can be due to such things as errors of measurement, recording, or reconstruction of specimens, the fragmentary nature of the fossils, or the fact that specimens are not necessarily a representative sample of the population.

Growth Factors

Individual differences can arise through differential rates of growth of certain parts of the body relative to others, but since variation is affected by the interaction of functional complexes, a change in one area can cause changes in another area. The evolution of morphological characters which differentiate between species is achieved through alterations in the inherited pattern of growth and development. Since functional systems can evolve at different rates then fossils sampled from different times may show differences caused by only slight changes in one aspect of morphology. Conversely, if morphological differences are the result of genetic changes which have influenced the timing of gene expression during growth and development, they could produce substantial changes in the phenotype. Thus individual differences in morphology can happen because of differential variations in the rate of development of different structures but this process can also produce the kind of differences seen between different species or genera (Harrison *et al.* 1983).

An additional source of variation which needs to be considered is that resulting from allometric growth changes. Allometry describes the change in proportions brought about by changes in size. Allometric growth involves changes in shape that come about because of differential rates of growth in body parts. Thus changes in morphology could occur because of changes in size resulting in an alteration of relationships between different parts and functions of an organism (Simpson 1953; Gould 1977). Thus growth, involving both changes in size and shape, plays an important part in the development of individual differences but also in the evolution of morphological characters and must be taken into account when assessing within-group variation.

Environmental Factors

The interaction between a community and its total environment requires the adaptation to that environment of individuals within a group. These interactions can involve biological processes affecting the function, form, and growth of individuals but also ecological factors such as habitat, diet, and social interactions. These factors can affect different populations of the same species differently if the geographical distribution is wide enough over a long enough period of time. Since populations within a species adapt to their local environment, not every population of every species will be identical. Each local population is the product of continuing selection and of geographical variation of the environment and so can differ somewhat in morphological characters, behaviour, and diet (Mayr 1963). Thus the degree of difference between populations can vary over the range of a species and over time, and this variability must be recognised when classifying the fossil hominids.

Sexual Dimorphism

The study of sexual dimorphism is made more difficult because the factors of individual and geographic variation must be eliminated before sexual dimorphism can be said to be the cause of variation within a group. This requires carefully documented samples, not always available, even for modern species.

Recently there have been a number of studies examining patterns of sexual dimorphism in primate crania and dentition (Wood 1975, 1976a; Holland 1986; Uytterschaut 1986; Oxnard 1987) which have resulted in disagreements about the variability of patterns of dimorphism. Wood (1976a:32) found that "Apart from a few exceptions variables are consistently sexually dimorphic in all groups, differences between primate groups being one of degree of dimorphism rather than due to a different pattern of dimorphism." Oxnard (1987) however found greater differences between patterns of dental sexual dimorphism between hominoids and O'Higgins (1989a) found differences between patterns of cranial dimorphism between hominoids. Thus there is some debate about the degree to which patterns of sexual dimorphism differ between hominoids. Some researchers follow the practice of using the ratio of female to male means of extant hominoids as a measure of dimorphism to be expected within fossil groups (eg. Lieberman *et al.* 1988) where the ratio of extreme values of fossils are used. To do this one assumes that a "difference between the size extremes in the fossil sample mirrors the mean difference between the sexes. This method... implicitly assumes no overlap between the sexes" (Kimbel and White 1988). According to Krantz (1982:95) "One should not assume that the ancestors of each of the living hominoid species necessarily showed the same kind and degree of sexual dimorphism as their living descendants. Similarly, if sexual dimorphism can be established in fossil forms, it does not automatically follow that their descendants (including living species) should all follow the same pattern." Therefore the pattern of fossil sexual dimorphism may not be determinable, but the degree of sexual dimorphism found within modern species can be used to place some limits on the amount of variation due to sexual dimorphism to be expected within samples of fossil hominids.

Variation over Time

The study of variation in the fossil hominid record has important implications for the understanding of speciation. Species are biological entities which are united as a cohesive unit by gene flow which has a homeostatic effect upon the combined gene pool (Bonde 1977). Change in gene frequency, or evolution, takes place by selection for or against characters where selection can be stabilising, directed or disruptive with respect to the range of variation of a species. Stabilising selection effects the extremes of the range, reducing variation in favour of the mean value of a character (or phenotype). Directed selection may effect only one extreme of the range, causing a shift in the mean or average, while disruptive selection effects the mean only, resulting in a bimodal distribution of a character (or phenotype). All three kinds of selection can act to change gene frequencies within the gene pool of a species (Berry 1982).

Under stabilising selection the boundaries of variation are limited but times of environmental instability can result in a change in gene frequency. Following a period of change there may be an increase in diversity to adapt to the new environment (may involve adaptation to new niches); maintenance of low variability or specialisation; or the inability to adapt to the new environment, leading to extinction. If the species is to survive under new conditions there is a 'choice' between low variability, favouring the survival of more individuals in the short term but potentially fatal if conditions change, and wide variation favouring survival in the long term. (For a contrasting view of large scale evolutionary events see Chapter 7).

The fact that the amount of variability within and between species can change over time due to changing environments or the movement of species into different niches/ geographical areas needs to be considered when assessing fossil hominid variation. If specimens of the same species are obtained from different time periods so that individuals from stable and non-stable environments are combined in the same sample, an increase in the amount of variability for the species as a whole may result, which would not be an indication of speciation. Thus instead of viewing slight variations as indicating the presence of a new species it may be better to follow a populational approach where wider ranges of morphological variation are tolerated within a single species. Thus I agree with Tattersall (1986) that if distinct morphs are **readily** recognisable they should be assigned to different species, but not if the differences can be shown to be due to differences in age, sex, regional ecological differences, or change over time within a species.

1.2.2 Inter-specific Variation

Between-species variation is usually thought of as relating to species as a whole rather than to individuals though it is a property of both. It may be viewed as a product of selection rather than material for selection and it is not transferable from one group to another. The causes of inter-specific variation are primarily genetic and include: morphological adaptations to the environment; allometric variation reflecting differences in body size between groups; pleiotrophic variation involving covarying characters, some of which may be of neutral value; plesiomorphic variation (Chamberlain 1987) involving characters inherited by descendants of a common ancestor which may be of neutral adaptive value; and stochastic variation involving mechanisms of evolution such as gene drift or founder effects.

1.3 Aims and Approach

1.3.1 Introduction

It has been common practice in the past to use the variability found within extant hominoid groups as a measure of the amount to be expected within fossil groups. When variability within the fossil groups exceeded that of the modern groups the homogeneity of the former was questioned, whereas when it did not no case for specific distinction was made.

Before within- and between-species variability can be assessed species limits must be determined, but once the species has been defined then statements can be made about patterns of variation within and between groups. One method of achieving this is to attempt to find characters that are stable within groups, ones which should not be affected by differences between individuals, sexes, or geographical morphs of the same species, but can distinguish between groups. Some characters are highly variable, reflecting either loss of function of that character or being ones for which mechanics and function are less rigidly integrated, while some characters are less variable indicating that stabilising selection is acting on them more strongly. Characters which have low variability within groups but high variability between groups are said to have high 'phyletic valence' (Robinson 1960, 1965; Tobias 1967, 1985) and would best be able to discriminate between groups. Characters of low within-group variability are likely to be ones least affected by differences in sex and other causes of variation and so may also help to discriminate between groups. In comparison, highly variable traits are less likely to be able to discriminate between groups or between sexes. Thus it would be useful to try to distinguish between these types of characters and to determine their utility in testing the homogeneity of groups, discriminating between sexes, and discriminating between groups.

3.1.2 Aims

The aims of this thesis are threefold:

1. To examine patterns of morphological variation in the crania of extant species (*Pan*, *Gorilla*, *Pongo*, and *H. sapiens*) to determine if any common pattern of primate sexual dimorphism exists which could be used in the assessment of fossil hominid sexual dimorphism;

2. To examine patterns of between species variability among the crania of the above extant species to determine if characters exist which could be useful as taxonomic indicators, especially of specific distinctiveness in fossil Hominidae; and

3. To assess the validity of using traits which are dimorphic and/ or variable within species as taxonomic indicators in systematic analyses.

3.1.3 Approach

The morphological variation in extant species is used as a guide to variation to be expected within and between the fossil hominid species. Patterns of cranial variation are examined within *Pan*, *Gorilla*, *Pongo*, and *H. sapiens* to provide comparative data for the study of within- and between-group variability of certain fossil hominids and to investigate whether knowledge of patterns of variation in extant hominoids may be used to illuminate patterns of fossil hominid cranial variability. Thus an attempt will be made to find characters of systematic and functional importance generally applicable to problems of hominid taxonomy and phylogeny.

Chapter 2 involves a review of the available literature with the purpose of: 1) defining the fossil hominid species used in this thesis; 2) discussing their distribution in time and space; and 3) discussing current views of their phylogenetic relationships.

The third chapter contains a review of statistical methods and techniques of cladistic analysis employed in this study. The section on statistics provides an overview of procedures available for the analysis of cranial variability and a justification for the techiniques used in this study. A review and critical appraisal of cladistic analyses follows, focussing on those studies primarily directed towards analysis of hominid and hominoid phylogeny.

The chapter of Materials and Methods lists the fossil hominids as well as outlining the characters used in the present study. Characters were chosen from different regions of the skull to allow the inclusion of fragmented fossil specimens and more detailed analysis, and then quantified to assess within- and between- species cranial variation. The skull was divided into five regions, two of these (the mandible and palate) forming part of one functional complex: the masticatory system. The masticatory system, base, vault, and face are each represented by roughly the same number of measurements although some measurements cross regional boundaries. The choice of characters was influenced by those commonly found in the literature (eg. Howells 1968; Dean and Wood 1981, 1982; Chamberlain 1987). The section on methods explains the statistical and cladistic analyses used to assess the patterns of morphological variation within and between extant hominoid and fossil species.

To fulfil the first two of the three aims of this thesis, univariate and multivariate statistical analyses were performed. The range of variation in samples of extant primate species was examined using univariate methods in order to ascertain the maximum range of variation to be expected within the fossil groups. This involved the use of sample statistics such as the mean, variance, standard deviation, coefficient of variation, and percentage sexual dimorphism, allowing quantitative comparisons to be made within and between groups and between individuals on the basis of their variability in individual characters. Such methods allow the inclusion of fragmentary fossil specimens in the sample, so giving a better measurement of group variability for any particular character. Although this method assumes that fossil fragments have been correctly assigned to the appropriate taxon it is useful for detailing any patterns of variation within and between groups of fossil hominids and extant hominoids.

Multivariate analyses are also used to assess inter- and intra-species variation. The main benefit of multivariate techniques is their ability to identify and quantify patterns of overall morphological similarity between crania or individual morphological regions. However, given the limited and fragmentary nature of the hominid fossil record the number of characters common to individual fossils is small, so reducing the number of characters available to discriminate within and between hominid species.

A number of questions arose in the consideration of the third aim of this thesis. For instance, if morphological characters are variable within modern groups, and if they are also dimorphic, are they really useful yardsticks with which to assess group homogeneity or to act as taxonomic indicators? What effect do they have on assessments of phylogenetic relationships? Tobias (1989) discusses ways that non-metric traits have been used mistakenly in cladistic analyses because only one individual was used to represent the species and within-group variation had not been taken into account. Rak (1988) also points out the misuse of non-metric traits in cladistic analyses stating that the presence or absence of a trait implies close relationship of two species only if the character is present or absent for the same reason.

I see a similar problem with metric traits in cladistic analyses. Within a sexually dimorphic species, it is possible that for any one dimorphic character the male range may not overlap the female range, so the mean value of both sexes combined does not represent the species, and may not even exist in nature. Also, if the range of values for any one character is large, either within each sex or within the combined sample, the mean value will not necessarily be representative of the species. So when a trait is known to be highly variable within a group and/or within sexes and/or highly dimorphic its usefulness as a taxonomic indicator comes into question. If these types of characters are used in cladistic analyses they may effect the composition of the clades and the relationships between them.

With this problem in mind, I compare below in Chapter 7 the results of using variable/ dimorphic traits versus non-variable, non-dimorphic traits in cladistic analyses using methods and programs that have been used by previous researchers. The purpose of this analysis is to determine which of these different kinds of characters results in the most parsimonious cladograms and the effect such characters have on the relationships between clades within the cladograms.

Thus the present study involves an analysis of inter- and intra-specific diversity among the early hominids based on models derived from samples of modern humans and pongids. Metrical and morphological cranial characters are surveyed in order to assess the functional and systematic/ phyletic implications of their variability within the available early hominid sample using univariate, multivariate, and cladistic analytical techniques.

The final chapter contains a reassessment of these aims and an evaluation of how successfully they have been met in the present study.

CHAPTER 2: HISTORICAL REVIEW OF THE FOSSIL SPECIES

2.1 Introduction

Most researchers recognise two genera of hominids: *Australopithecus* and *Homo*. The former genus includes a number of genera as junior synonyms: *Plesianthropus* Broom, 1937a; *Paranthropus* Broom, 1938a; *Zinjanthropus* Leakey, 1959; and *Paraustralopithecus* Arambourg and Coppens, 1967. Most workers accept four species of *Australopithecus*: *A. africanus*, *A. afarensis*, *A. robustus*, and *A. boisei* but some recognise *A. crassidens* as a separate species from *A. robustus* (Howell 1978a; Grine 1981, 1985a, b, 1988a, b; Jungers and Grine 1986) and some of the recent fossils from West Turkana, Kenya may represent an additional species *A. aethiopicus* (Walker *et al.* 1986; Delson 1986, 1987; Walker and Leakey 1988; Kimbel *et al.* 1988). The retention of *Paranthropus* as a separate genus for 'robust' species of *Australopithecus* has gained support from a number of workers (eg. Olson 1985; Dean 1986; Wood and Chamberlain 1986; Grine 1988b).

The genus *Homo* also includes a number of genera as junior synonyms including *Pithecanthropus* Dubois, 1894, *Sinanthropus* Black, 1927, *Meganthropus* Weidenreich, 1945, and *Telanthropus* Broom and Robinson, 1949b. The species recognised within *Homo* are *H. habilis*, *H. erectus*, and *H. sapiens*. Subspecies are recognised within these species but their composition and homogeneity is the cause of disagreement between workers.

The following sections outline the location of the above species and genera, of which some specimens are included in this thesis and include a review of the current arguments over the relationships between them.

2.2 South African Australopithecines

The fossil hominids from South Africa are found at 5 sites: Taung, Sterkfontein, Kromdraai, Swartkrans, and Makapansgat. The dating of these sites is uncertain since they cannot be dated using potassium-argon techniques. A number of techniques have been used in the past to date these sites but most have been unsuccessful (eg. Partridge (1973) using a geomorphological approach) but Cooke (1970) used faunal comparisons which have provided dates that are generally accepted (eg. Tobias 1978). The oldest sites are Makapansgat: 2.5 - 3.0 million years (m.y.) (Cooke 1970); 3.7 m.y. (Partridge 1973- the earliest opening of the cave) and Sterkfontein: 2.5 - 3.0 m.y. (Cooke); 3.3 m.y. (Partridge). Swartkrans was given a date of 2.0 m.y. by Cooke and 2.6 m.y. by Partridge, while Brain (1988) gives a date for Member 1 of 1.7 m.y. Tobias (1976:403) estimates that Kromdraai is approximately 1.5 - 2.0 m.y. Taung has been dated to less than 0.87 m.y. by Partridge; a date that was supported by Butzer's (1974) work, however, Delson (1988) gives a date of 2 to 3 m.y. for Taung. Other faunal dating methods (eg. Vrba 1975a and b) show that Sterkfontein and Makapansgat are the oldest sites followed by Swartkrans and then Kromdraai.

In 1925 Dart announced the discovery of a young juvenile from a site called Taung in South Africa which he assigned to the new genus and species of *A. africanus.* He described features which led him to conclude that his specimen was "...intermediate between living anthropoids and men... " (1925a) and tentatively proposed a new family, Homo-simidae, to accommodate it. He was supported by Broom (1925, 1930) but challenged by Keith (1925a and b) while other prominent anthropologists of the time remained sceptical and awaited further details (Elliot Smith 1925; A. Smith Woodward 1925; Duckworth 1925 see also Dart 1925b). Hrdlicka (1925) maintained that adult specimens were needed to confirm Dart's assertions. Broom searched for additional fossils to confirm the status of *A. africanus* and in 1936 found an adult fossil at Sterkfontein. He stated that "This newly found primate probably agrees fairly closely with the Taungs ape..." (1936a:488). Because it was from a different time period from Taung Broom assigned it to a different species *A. transvaalensis* (Broom 1936a and b, 1937a and b). In 1938 Broom found a new mandible at Sterkfontein which he felt was significantly different from Taung to warrant placing specimens from this site into a new genus, *Plesianthropus transvaalensis* (1938a, c, 1941). He also discovered a new specimen from Kromdraai which he named *Paranthropus robustus* since its teeth differed from *Plesianthropus transvaalensis* and it was from an apparently older deposit than the specimen from Sterkfontein (1938b:378). In 1948 at Swartkrans, Broom found another robust type of fossil which he named *Paranthropus crassidens* (Broom 1949). Dart (1940) continued to uphold his original statements concerning *A. africanus* and in 1948 discovered a new fossil at Makapansgat which he called *A. prometheus.* Specimens continued to be found and reported on from all sites but Taung (Broom and Robinson 1947, 1949a and b, 1950, 1952; Dart 1948a, b, c, 1949, 1954a, b, 1955a, b, 1959a, b, 1962; Dart and Bone 1955; Gregory and Hellman 1939; Robinson 1954b, 1956). From 1950 onward arguments continued about the number of species and genera at these South African sites (Broom 1950; Mayr 1950; Washburn and Patterson 1951; Robinson 1954a, 1963a, b, 1972; Brace 1969, 1973; Campbell 1974; Wolpoff 1971a, b, 1974a, 1978; Le Gros Clark 1964a, b, 1967).

Tobias (1967) and others (eg. Bilsborough 1972, 1986; Rak 1983) recognised two

South African species *A. africanus* and *A. robustus.* Dean and Wood (1982), however, pointed out differences in the basicrania of gracile and robust hominids and Dean (1986) states that these differences provide evidence for regarding *Australopithecus* and *Paranthropus* as separate genera. Wood and Stack (1980) show that the dental differences between gracile and robust hominids are not allometric; that the difference in dental proportions is not just a scaling effect and may reflect different adaptations of diet or social behaviour. Grine (1988b) points out that stressing *Australopithecus* as a grade of organisation implies that 'gracile' and 'robust' species are scaled variants of one another. Since Jungers (1988) and McHenry (1988) have found that body size in both groups are not as different as was once thought Grine (1988b) suggests that the terms 'gracile' and 'robust' be dropped from the literature.

On the basis of different dental development some authors (eg. Beynon and Dean 1988) would now distinguish between robust and gracile hominids at a generic level (ie. *Paranthropus* and *Australopithecus*) and Grine (1981) and Jungers and Grine (1986) maintain that Swartkrans and Kromdraai robust hominids are biologically distinct, probably at the species level, based on molar wear patterns and this may support the revival of *A. crassidens* although the sample of 'robust' hominids from Swartkrans is homogeneous (Grine 1988a).

Kimbel and White (1988) believe that the specimens of *A. africanus* show greater variability than that found in *A. afarensis* and suggest this is due to taxonomic variation and Clarke (1988) outlines evidence which seems to support this view.

Tobias (1973, 1978) presented chronological and morphological data which suggested that the Taung baby may be *A. robustus* based on dates for Taung given by Partridge (1973). Butzer (1974) maintained that the Partridge's dates were meaningless and later studies (eg. Olson 1985, Grine 1981, Dean and Wood 1982) showed that the Taung child was indeed *A. africanus* and that Tobias's claims were unfounded. Tobias now (1988, 1989) believes that the Taung child may represent a derived form of *A. africanus* ancestral to *H. habilis*, *A. robustus*, and *A. boisei.*

2.3 East African Australopithecines

2.3.1 A. boisei

In 1959 a new australopithecine skull was found at Olduvai Gorge in Tanzania which Leakey (1959, 1960) referred to as *Zinjanthropus boisei* (OH5). Robinson (1960) noted this specimen's affinities with *Paranthropus* and Tobias (1967) considered it to be a distinct species of australopithecine: *A. boisei.* Some authors (eg. Robinson 1960; Bilsborough 1978) believed that *A. boisei* and *A. robustus* were too close morphologically to be separated into two species. Tobias (1976:401) has suggested combining *A. robustus* and *A. boisei* into one 'superspecies ' but Rak (1983) demonstrated clearly that *A. boisei* '...exhibits a different topography of the facial mask as well as a distinct architectural pattern'.

Since 1959 a number of other specimens have been found in East Africa and referred to the same species. There is a partial cranium from Chesowanja, Kenya (Carney *et al.* 1971), a mandible from Peninj, Tanzania (Leakey and Leakey 1964), several mandibles, a cranium, and some teeth from Omo, Ethiopia (Rak and Howell 1978), and a number of specimens from East and West of the Lake Turkana Basin (eg. Leakey 1970). *A. boisei* dates from 2.5 m.y. to about 1.4 m.y. in the Lake Turkana Basin (Leakey and Walker 1988) and to about 1 m.y. at other sites.

Recently, a new cranium (KNM-WT 17000) and mandible (KNM-WT 16005) found West of Lake Turkana, Kenya have been dated to 2.5 m.y. (Walker *et al.* 1986, Leakey and Walker 1988). Walker *et al.* (1986:520) argue that this specimen can be included in *A. boisei* and list a number of craniodental character states of various australopithecines to support this opinion (Walker and Leakey 1988; Walker 1989). Delson (1986:497) disagrees and believes that KNM-WT 17000 may represent a population of hominids near the divergence of South and East African robust australopithecines since it has several characters which are typical of both *A. robustus* and *A. boisei.*

Walker *et al.* (1986) also argued that this new evidence makes it impossible for *A. boisei* to have evolved from *A. robustus.* Delson cautions that it is still possible that a form like *A. robustus* could have been present between 3 and 2.5 m.y. ago which gave rise to members of the robust lineage (1986:497). The new cranium is similar to *A. afarensis* in a number of features and Walker *et al.* (1986:521) suggest the possibility that the *A. afarensis* specimens (like Olson 1981, 1985) include two species, one of which gave rise to *A. boisei.*

Walker and Leakey (1988) note the differences between KNM-WT 17000 and later *A. boisei* specimens may warrant specific distinction but believe KNM-WT 17000, KNM-WT 16005, and Omo 18-1967-18 to be of the same species. This latter specimen, a mandible, was named *Paraustralopithecus aethiopicus* by Arambourg and Coppens because of differences between it and specimens of *A. robustus* and *A. boisei.* Wood and Chamberlain (1986) would place Omo 18-1967-18 in *A. boisei* while Kimbel *et al.* (1988) would allocate KNM-WT 17000 and the Omo mandible to the same species, *Australopithecus* or *Paranthropus aethiopicus.* Grine (1988a) maintains that the attribution of KNM-WT 17000 and Omo 18-1967-18 to the same species is spurious but would not place the former in *A. boisei* while Kimbel *et al.* (1988) point out a number of morphological differences between KNM-WT 17000 and other robust specimens and show how it resembles *A. afarensis.* Suwa (1988) provides dental evidence to show how specimens from Omo from below Member G of the Shungura formation are different from *A. boisei* specimens and provides evidence for the presence of a separate species in East Africa between 2.6 to 2.3 m.y. while Uytterschaut and Wood (1989) demonstrate major differences between the East African 'robusts' and other taxa on the basis of premolar morphology. Also, Dean (1988) even suggests from mandibular measurements that a third species can be recognised within the *A. boisei* hypodigm. Thus the new fossils from East Africa may require that four species of 'robust' australopithecines be recognised.

2.3.2 A. afarensis

In 1939 Kohl-Larsen found the first hominids at Laetoli. They were fragmentary, the largest being part of the maxilla with two premolars which was subsequently named *Meganthropus africanus* by Weinert (1950 in Wood 1978). Initially there was a debate over which specimens **M. africanus** most resembled *M. palaeojavanicus* from Java or *A. africanus.* Robinson (1953a, 1954a, 1955) maintained that *M. africanus* = *A. africanus.* Remane (1954) felt that *M. africanus* was a very primitive hominid, that its premolars were nearer to pongids and doubted that *M. africanus* was the same species as *Plesianthropus* whereas Robinson (1955) argued that calling the East African specimen *Meganthropus* was unjustified since there were only lower premolars from Java and upper premolars from Laetoli and that the Laetoli specimen matched specimens from Sterkfontein. In 1974 and 1975 Mary Leakey made further explorations at the site of Laetoli and found dental and gnathic remains which were felt to sample one population despite the variation in size within the sample (Leakey *et al.* 1976; White 1980b). In 1973 and 1974 the International Afar Expedition discovered the remains of some new fossil specimens at Hadar in Ethiopia which were later combined with the Laetoli specimens, including the *M. africanus* specimen, to form a new species *A. afarensis.*

The Pliocene site of Hadar is located in Ethiopia about 300 km northeast of Addis Ababa in the west central Afar basin, while Laetoli is located in Tanzania about 50 km south of Olduvai Gorge (Johanson 1980). Fossil specimens assigned to the taxon *A. afarensis* were recovered from Hadar, Ethiopia from a time period ranging from approximately 2.9 to 3.2 m.y. with some suggestion of earlier dates (Brown 1982; Hall, Walter, Westgate, and York 1984; Schmitt and Nairn 1984), and from Laetoli, Tanzania, which date to between 3.6 and 3.8 m.y. (White 1980b). Detailed descriptions and measurements of these fossils have been published (M. D. Leakey *et al.* 1976; White 1980b; and Johanson *et al.* 1982). Although initially it was thought that more than one species was represented at Hadar (Johanson and Taieb 1986), later articles propose that the material from Hadar and Laetoli represents one species (Johanson, Taieb, Gray, and Coppens 1978; Johanson, White, and Coppens 1978; Johanson and White 1979, 1980; Johanson 1980; White, Johanson, and Kimbel 1981; Delson 1981; White and Johanson 1989; Johanson 1989a).

It has been maintained that although *A. afarensis* specimens can be linked via a few of their morphological characteristics to the South African species *A. africanus*, they "...have a distinctive suite of cranial and postcranial characteristics... [and] ... the morphology and attributes of these remains are demonstrably more primitive than those of hominid specimens from other sites" (Johanson and White 1979:321). A comparison of dental, cranial, and postcranial characteristics between *A. afarensis*, *A. africanus*, and *A. robustus* + *boisei* led White *et al.* to propose an alternative phylogeny for the African hominids. They maintained that:

> ...although *A. afarensis* and *A. africanus* share many common primitive features, the latter taxon exhibits a morphological composite of the skull and dentition derived toward the *A. robustus* + *boisei* character state... members of the *Homo* clade do not show this specialization... (1981:466).

They were supported by Rak (1983, 1985a, b) who demonstrated the derived facial characteristics of *A. africanus* and *A. robustus* + *boisei.*

In 1979 Johanson and White proposed that *A. afarensis* was a common ancestor of the later hominids and that *A. africanus* was the ancestor of *A. robustus*+ *boisei.* They believed that the most parsimonious phylogeny was one in which *A. afarensis* led to *A. africanus* and *A. robustus*/*A. boisei* on one branch and to *Homo* on the other. They maintained that if *A. africanus* was ancestral to both *Homo* and the robust australopithecines it would mean that a number of derived mandibular, dental, and facial characteristics must have reversed to produce those found in *H. habilis* (White *et al.* 1981:467). Unfortunately, there does not seem to be direct evidence to link *A. afarensis* to *H. habilis.* Indeed, these authors admitted that: "in the absence of clearcut evidence to the contrary, we have directly linked successive taxa in each of the two major hominid clades " (1981:467). These authors believed, however, that hominids intermediate to *A. afarensis* and *H. habilis* would be found that did not exhibit the morphological pattern of *A. africanus* (1981:467).

The homogeneity of *A. afarensis* and its status as a common ancestor to later hominid lineages while supported by a number of authors has been challenged by some who believe the following points need substantiation:

1. that the material from Hadar and Laetoli can be linked together to form one species;
2. that there is sufficient difference between *A. afarensis* and *A. africanus* to warrant a new taxon; and
3. that the Hadar material is homogeneous.

The first two points have been challenged by Tobias (1980a) in particular. He demonstrates that the characteristics which Johanson *et al.* (1978) argue distinguish *A. afarensis* and *A. africanus* are in fact not unique. Indeed he maintains that there is not enough evidence to distinguish between them on a species level. He states emphatically: "In a word '*A. afarensis*' cannot be separated from *A. africanus* on the characters that have been adduced as the diagnosis" (1980:9). Bilsborough (1986:211) agrees that there is an "... extensive overlap between the africanus and afarensis samples". Apart from the fact that these two sets of material are separated in time (the oldest of the Laetoli hominids being possibly one million years older than the the youngest of the Hadar hominids) Tobias (1980a:12) found that metrically and morphologically each sub-set resembled *A. africanus* more than each group did to each other. For this reason Tobias (1980a:14) would separate the two samples on a sub-species level. He proposes the name *A. africanus afarensis* for the Laetoli material (since the holotype of *A. afarensis*, LH 4, comes from this site) and *A. a. aethiopicus* for the Hadar material.

McHenry and Corruccini (1980:1104) supported Johanson and White's (1979) evolutionary scheme which displaces *A. africanus* as common ancestor to *Homo* on the basis of crown component measurements of extant and fossil hominoids' mandibular molars. White's (1985) comparative analysis of the dentition from both sites demonstrated that these samples were united by their possession of a large number of primitive characters with any differences due to intra-specific variation and/or sampling error. White states that the conspecificity issue is "...easy to resolve on the basis of present samples..." (1985:150). Grine (1985a) examined the deciduous teeth of a number of different hominid samples and found differences between *A. africanus* and *A. afarensis* on the basis of the distributions of deciduous crown morphology. He maintains that his evidence supports the distinction of *A. afarensis* from *A. africanus.* Ferguson (1987), however, rejects the homogeneity of the *A. afarensis* sample on the basis of dental evidence. Thus there is conflicting dental evidence concerning the conspecificity of the *afarensis* material and its relationship to *A. africanus* and the other hominids.

Olson (1981, 1985) examined aspects of the cranial morphology of the Pliocene hominids, specifically, the occipitomastoid and nasal regions and found that some of the Hadar specimens (eg. A.L. 333-45 and 333-105) possess derived robust features in the nasal region and basicranium which he groups under the name of *Paranthropus africanus* (1985:114-5). The remaining Hadar specimens, including A.L. 288-1, are thought to be primitive members of the *Homo* clade and are called *Homo (Australopithecus) aethiopicus* (1985:117).

Kimbel *et al.* (1985:120) maintain that Olson's (1981) interpretation of two taxa at Laetoli and Hadar can be disproved both metrically and morphologically. They believe that Olson has misinterpreted the morphological variation existing in the mastoid region among the *afarensis* material and later hominids and argue that Olson has made several errors in his analysis of the cranial base. Kimbel *et al.* believe that there are no features of the *A. afarensis* mastoid region that indicate specialisations shared with the robust lineage. Also, features of the nasal region resemble the African ape condition and thus are primitive rather than specialised (1985:136). Thus these authors deny the presence of two species at Laetoli and Hadar and support the retention of the taxon *A. afarensis.* However, Schmid's (1989) comparison of A.L. 288.1 to the reconstructed *A. afarensis* cranium showed that the differences between them were due to allometric size difference and species difference.

White (1980a) and Day and Wickens (1980) have demonstrated that Pliocene hominids were bipedal; a view derived from the discovery of hominid footprints at Laetoli. Since then, Stern and Susman (1983) and Susman *et al.* (1984, 1985) have examined aspects of the postcranial anatomy from Hadar to determine to what extent other forms of posture and locomotion made up a part of early australopithecine behaviour.

Susman *et al.* maintain that certain aspects of the postcranial skeleton, especially the lower limbs and feet, indicate that Hadar hominids utilised behaviours of both arboreal climbing and terrestrial bipedality (1985:185). It should be noted, however, that Tuttle (in Stern and Susman 1983:309) believes that the feet from Hadar and the Laetoli footprints do not correspond.

Senut and Tardieu (1985:193) have examined the elbow and knee joints of various Plio-Pleistocene hominids including those from Hadar in order to assess their "...morpho-functional, taxonomic, and phylogenetic implications". A comparison of elbow and kneejoint morphology indicates that in one group (thought to be members of early *Homo*) the kneejoint was more rigid and the elbow joint more lax. In the second group, referred to as early *Australopithecus*, the opposite is the case. Senut and Tardieu believe that "...suspension or climbing could have been important for *Australopithecus* (and especially *A. afarensis*) and that its bipedalism was probably different form ours" (1985:199). Thus the evidence of elbow and kneejoint morphology does not support the presence of a single species at Hadar.

Stern and Susman (1983) note that features indicating climbing adaptations are not found in later australopithecines and *Homo*. If *A. afarensis* is the direct ancestor of these later forms then either a parallel evolution of more modern locomotor adaptations occurred or there must have been an intermediate form which evolved with these adaptations after *A. afarensis* but before the separation into two lineages. Bilsborough (1986) states that neither scenario is likely and suggests instead that *afarensis* and *africanus* are either chronospecies within one lineage and separation occurred subsequent to their development, or else Tobias's 1980a separation of *A. afarensis* into two sub-species is a more parsimoneous interpretation of the evidence (1986:211).

Day (1986:93) in his summary of the 1984 sessions on Plio-Pleistocene hominid anatomy at the American Museum of Natural History notes that the Berkeley group, who support a single species at Hadar, did not contest the evidence of the postcranial anatomy. He states that "...it was left for us all to decide whether the special pleading for a wider range of Hadar sexual dimorphism than previously known in primates is a convincing position to sustain". But recently Lovejoy *et al.* (1989) found the variation present in the *A. afarensis* postcranial material fell well within the range of sexual dimorphism of modern species.

2.4 Phylogenetic Considerations

The phylogeny proposed by Johanson and White (1979) is no longer tenable on the basis of the new West Turkana evidence. Most workers believe that specimens from Kromdraai and Swartkrans are closely related as are the East African forms (KNM-WT 17000 and later *A. boisei*) but the relationship between the eastern and southern forms are in doubt. Wood (1988) states that although robust australopithecines as a monophyletic group is the most parsimonious hypothesis the fact that they may be paraphyletic cannot be dismissed. He also states that functional complexes like the masticatory system may have evolved convergently or in parallel. Thus it may be that *A. robustus/ crassidens* evolved from *A. africanus* and *A.boisei/ aethiopicus* from *A. afarensis.* Grine (1988b) argues, however, that some features shared by eastern and southern African robusts are not linked to mastication and are more likely to be synapomorphic than convergent. He maintains that the case for monophyly is the stronger hypothesis and proposes the use of *Paranthropus* for that lineage.

As mentioned previously KNM-WT 17000 shares a number of synapomorphies with *A. robustus* and *A. boisei* as well as symplesiomorphies with *A. afarensis* which suggests a link between *A. afarensis* and the robust australopithecines to the exclusion of *A. africanus.*

Clarke (1985:176) demonstrates that *H. habilis* and *A. africanus* share many morphological similarities. Also, Dean and Wood (1982:157) demonstrate that there are a number of significant differences between the cranial base patterns of robust and gracile hominids. Skelton *et al.* (1984) argue that *A. africanus* and the robust australopithecines share a number of derived characters with *H. habilis* that are not found in *A. afarensis.* Thus there is some evidence to support the hypothesis that *A. africanus*, not *A. afarensis*, is the most recent ancestor of *H. habilis* though the similarities between *A. africanus* and *A. afarensis* have been outlined previously (Tobias 1980a; Bilsborough 1986). The new specimens from Kenya are thought, by at least one author (Delson 1986), to indicate separately evolving lineages of 'gracile' and 'robust' hominids with a common ancestor in *A. afarensis* which would mean that the similarities shared by *A. africanus* and *A. robustus* must have evolved in parallel.

2.5 Discussion

In South Africa there is one gracile species recognised but the possibility of a second one has been suggested on the grounds that *A. africanus* is too variable to be a single species. Also, the possibility of two robust species has increasing support in the literature. Either all these specimens belong in one genus or else two genera are needed to explain their phylogenetic relationships. In East Africa *A. boisei* is present from 2.5 to about 1.4 m.y.; a highly sexually dimorphic lineage which shares some characteristics with *A. afarensis* or else two closely related species are present in this area. The validity of the taxon *A. afarensis* has been questioned by a number of workers on the basis of dental, cranial, and postcranial anatomy. While there is some overlap between the characteristics of *A. afarensis* and *A. africanus*, some evidence suggests that their separation is a valid one but the validity of combining the Hadar and Laetoli material has not been proved. Thus although the taxonomic status and phylogenetic position of *A. afarensis* remains unresolved for the present the anatomical evidence, especially of the postcranial skeleton, suggests that two species of hominids existed at Hadar during the Pliocene.

There are currently two main hypotheses concerning early hominid phylogeny:

1. where *A. afarensis* leads to *A. boisei* (including KNM-WT 17000) and *A. africanus* leads to *A. robustus*, while the ancestry of *Homo* remains unclear; and
2. where *A. aethiopicus* is the sister taxon or ancestor of the later robust hominids and *A. africanus* is the sister taxon of *Homo* (Delson 1987).

The first hypothesis implies polyphyly of the robusts, the latter monophyly, but because *A. aethiopicus*, *A. boisei*, and *A. robustus* share a large number of features in common it may be better to support the latter hypothesis until the relationships between them are more resolved.

2.6 Homo habilis

2.6.1 East Africa

On the basis of new hominid material from Olduvai Gorge, Tanzania which dates from between 1.6 and 1.8 m.y. (L.S.B. Leakey 1961a, b; Davis 1964; Tobias 1964; Day and Napier 1964; Leakey and Leakey 1964) Leakey, Tobias, and Napier (1964) redefined the genus *Homo* and created a new species, *H. habilis*. This new species was considered to be ancestral to *H. erectus* and distinguishable from *A. africanus*. The type specimen is OH 7, an immature mandible associated with parietals and hand bones, the paratypes include OH 13, 8, 6, and 4, and referred material include OH 14 and 16. Also, these authors suggested that *Telanthropus capensis* may belong to this new species. Oakley and Campbell (1964) argued that if *Telanthropus* was like *H. habilis* then the name *capensis* would have priority over *habilis*. Since *capensis* was already occupied within the genus *Homo* (Broom called a skull from Boskop, Cape Province *Homo capensis*) it could not be used in this case but these authors cautioned care about the use of nomenclature when creating a new taxon.

Tobias and von Koenigswald (1964) compared *H. habilis* specimens to *Telanthropus* from Swartkrans and to some dental remains from Sangiran: OH 16 was thought to resemble the australopithecines not *H. habilis*; OH 13 resembled SK 15, Pithecanthropus IV, and Sangiran B; and the material from Bed I at Olduvai was said to be morphologically distinct from *Australopithecus* and *H. erectus.*

A number of workers questioned the validity of *H. habilis.* Campbell (1964) argued that there was insufficient morphological space between the australopithecines and *Homo* for a new species and felt that there was no more reason to call these specimens *Homo* than *Australopithecus.* Le Gros Clark (1964a) argued that the *H. habilis* material was *Australopithecus* since it was found in australopithecine deposits. His other objections include:

1. the cranial capacity of OH 7 could fall within the limit of the australopithecines and is much less than for *Homo*;
2. the frontal features of a strongly developed supraorbital ridge and pronounced post-orbital constriction were australopithecine characters;
3. the size and shape of the dentition was not sufficiently different;
4. the presence of tools is not evidence of *Homo*; and
5. the postcranial material is similar to that for *Australopithecus.*

Robinson (1965) maintained that the diagnosis of *H. habilis* was not complete and that:

1. the shape differences of the mandibular teeth of *H. habilis* do not fall outside the range of australopithecines;
2. characters used to distinguish *H. habilis* are of low phyletic importance;
3. the cranial capacity estimates were hardly different from those of the australopithecines;
4. the foot was not necessarily more advanced.

He maintained that the Bed I material was advanced *Australopithecus* and Bed II early *H. erectus.* Since the *H. habilis* material shared affinities with *A. africanus* and *H. erectus* Robinson advocated the transfer of *A. africanus* to *Homo* where *Homo* would consist of two species *H. transvaalensis* and *H. sapiens* since *africanus* was already used within *Homo.* Tobias (1965b) debated Robinson's claims and concluded that the premolars of *H. habilis* had a marked tendency toward buccolingual narrowing and mesiodistal elongation and that the lower premolars were absolutely narrower than those of the australopithecines.

Holloway (1965) supported Tobias' (1964) estimates of cranial capacity for OH 7 but thought that they could fall within an australopithecine range of variation.

Tobias (1965a) compared the australopithecine range of cranial capacity with extant great apes and argued that his calculations of the cranial capacity of OH 7 was at least three standard deviations above the estimated australopithecine mean. Tobias (1965b) continued to argue that a gap existed between the australopithecines and *H. erectus* and presented a phylogeny where *A. africanus* leads to *Homo* on the one hand and to *A. robustus* on the other.

Leakey (1966) still maintained that *H. habilis* was distinct but did not believe that the australopithecines gave rise to *Homo* since he believed that the cranial features of OH 13 resembled *H. sapiens* more than *H. erectus* and that OH 16 resembled *H. erectus.* Leakey concluded that possibly 2 species of *Homo* existed: one including OH 7 which gave rise to OH 13 which led to *H. sapiens* and another including OH 16 which led to *H. erectus.* Tobias (1965c) argued that OH 16 was an australopithecine but later includes it in *Homo* (1967, 1980a).

The argument between Tobias and Robinson concerning dental metrics and cranial capacities continued (Tobias 1966a; Robinson 1966). Tobias (1966b) and Holloway (1966) were still arguing over OH 7 and its taxonomic implications until in 1970 Holloway reassessed the South African values concluding that they were overestimated and thus supported the distinction of *H. habilis* from the australopithecines on morphological grounds.

Arguments over specimens

In 1969, M. D. Leakey (1969) announced the discovery of OH 24 from lower bed I which was said to resemble *H. habilis.* Leakey, Clarke, and Leakey (1971) maintained that OH 24 was like OH 13 but differed somewhat from OH 7 and concluded that there were either 2 forms of *Homo* in Bed I and II or else the differences were due to sexual dimorphism and individual variation. An editorial in Nature (1971) claimed that OH 24 could not be *H. habilis* because of its small cranial capacity and dished face but Tobias (1972) defended the inclusion of OH 24 in *H. habilis.*

At this time new fossils were beginning to be found at Koobi Fora in Northern Kenya, with most of the fossils from the Koobi Fora Formation coming from above or below the KBS tuff. Part of the confusion and controversy about what constituted *H. habilis* or if *H. habilis* really existed was the dating of the KBS tuff to 2.61 ± 0.26 m.y. (Fitch and Miller 1970, 1976; Bowen and Vondra 1973). Since specimens (like KNM-ER 1470) were found below the tuff and thus were older than it, it was thought that *A. africanus* could not be ancestral to *Homo.* New dates were found by using the potassium-argon dating method (Curtis *et al.* 1975) and these fell between 1.6

and 1.82 m.y. Since they corresponded to the faunal evidence they were felt to be correct. This meant that *A. africanus* could have been ancestral to *H. habilis*.

In 1970, R. E. F. Leakey reported a new cranium from Koobi Fora (KNM-ER 407) which he said was either a gracile species of australopithecine or early *Homo* but favoured the latter possibility. Leakey (1972) said that KNM-ER 817, 820, and 992 resembled *A. africanus* from Sterkfontein and implied that the remains at this site sampled both *Australopithecus* and *Homo*. Robinson (1972) maintained that the East and South African gracile hominids should be included in one species: *Homo africanus*. Leakey (1973a) reported 16 new specimens from above and below the KBS tuff which was still thought to be about 2.6 m.y. and these new specimens were assigned to *Homo sp. indet.* (1973b).

In 1974 more fossils were reported from Kenya including KNM-ER 1805 and 1813. Leakey (1974) speculated that the East African material included four genera consisting of:

1. robust;
2. gracile (OH 24, KNM-ER 1813);
3. *Homo* (OH 7, KNM-ER 1470, KNM-ER 1590); and
4. a primitive group including the KNM-ER 1482 mandible which he did not name.

Howell (1967) had proposed that specimens from Omo be called *H. habilis* but Boaz and Howell (1977) maintained that the 894-1 cranium from Omo shared affinities with the pre-erectus forms from Swartkrans, Olduvai, and Koobi Fora as well as with *Homo modjokertensis* from Java. If the Omo specimen proved to belong to the latter species these authors maintained that *H. modjokertensis* would have priority over *H. habilis*.

In 1975 Groves and Mazak divided up the East African material into two species based mainly on differences in the mandibular dentition. The first species included the material from Bed I and II at Olduvai and some specimens from Omo and was called *H. habilis*. A second, new, species was created called *H. ergaster*. Its holotype was the KNM-ER 992 mandible and included material from the upper member at Koobi Fora as well as KNM-ER 1805. These authors suggested that KNM-ER 1470 could be ancestral to *H. ergaster* but they do not distinguish the *ergaster* material from *H. erectus*. They only noted that in some cases the anterior dentition of the new species was similar to *A. africanus* and *H. habilis*. Chamberlain (1987:70) notes that since incisor size was used in the diagnosis of *H. habilis* to distinguish *H. habilis* from *A. africanus* "the value of this particular aspect of Groves and Mazak's diagnosis is questionable".

Leakey (1976a) maintained that some of the East African specimens including KNM-ER 1813 could be *A. africanus*. KNM-ER 1470 was felt to be the same species as OH 7 but Leakey did not support the use of *H. habilis*. Instead he felt that all the species of *Homo* could be accomodated in a series of grades of the two species *H. erectus* and *H. sapiens*. Walker (1976) examined the characteristics of KNM-ER 1470 and found that its features were mainly australopithecine ones. Walker and Leakey (1978:56) maintained that there was evidence for three contemporary species at Koobi Fora. In the lower member there existed one robust species, one gracile species like *A. africanus*, and *H. habilis*. In the upper member, not *H. habilis*, but *H. erectus* was present. Wood (1978) suggested that KNM-ER 1813 possibly belonged to a lineage separate from that of KNM-ER 1470 and 1590. Howell (1978b) revised the hypodigm of *H. habilis* and included most of the gracile hominids from the lower member of the Koobi Fora formation, some of the Olduvai material, the gracile Swartkrans material, and 894-1 from Omo.

Olson (1978) argued that some of the features of *Homo* included the separation of nasion from glabella and the continuity of the fronto-nasal and fronto-maxillary sutures but Eckhardt (1987) later demonstrated that nasal bone patterns were a polymorphic trait and consequently of little value as indicators of taxonomic affinity. Dean and Wood (1982) showed that *A. africanus* had a pongid-like cranial base but the robust australopithecines and African *H. erectus* had a more human-like base. They found that OH 24, SK 847, and ER 1805 had a combination of robust and *erectus/sapiens* features whereas KNM-ER 1470 and 1813 had bases similar to *H. erectus* (OH 9, KNM-ER 3733, and 3883). Wood (1985) later argued that the difference in cranial capacity of KNM-ER 1470 and 1813 meant that they could not belong to the same species. Bilsborough (1983) suggests that OH 16, KNM-ER 1805, and possibly KNM-ER 1470 may be sampling *H. erectus* prior to the stabilisation of the traditional *H. erectus* morphology but that OH 13, OH 24, and KNM-ER 1813 have few characters that indicate that they come from a pre-erectus population. He concludes that *Homo* may have been polyphyletic in its early stages.

Stringer (1986) divided the material into two groups. One group possessed some retained primitive features and a masticatory system paralleling features with the australopithecines but also derived *Homo* features and included KNM-ER 1470, 1590, 3732, 1802, 1481, 3228, OH 24, and OH 7; the latter specimen being included so that the group could be called *H. habilis*. The second group had features more like African *H. erectus* and *H. sapiens* and included KNM-ER 1813, 1805, OH13, OH 16, and possibly KNM-ER 992. Bilsborough and Wood (1988) found that the individual facial dimensions of *H. habilis* specimens usually fell within the range of *A. africanus* but concluded that these features considered together combine to form a different morphological pattern.

Chamberlain (1987, 1989) and Chamberlain and Wood (1987) show that shape variation in *H. habilis* exceeds that of extant species and divide the specimens into *H. habilis sensu stricto* (Olduvai) and *H. habilis sensu lato* from Koobi Fora, Swartkrans, and Sterkfontein. They maintain that the former group is relatively primitive while the latter shares affinities with the robust australopithecines.

The most recent find considered to be *H. habilis* is from Olduvai Gorge (Johanson *et al.* 1987; Johanson 1989b) consisting of an adult partial skeleton from Bed I (OH 62). The postcranial skeleton indicates a small body size and relatively long arms like early australopithecines and has similarities to A.L. 288-1 while the dentition, face, and palate show similarities to STW 53. Wood (1987) maintains that if OH 62 is *H. habilis* then the range of variation for specimens attributed to this species indicates great sexual dimorphism or else taxonomic variation. Leakey *et al.* (1989) propose that OH 62 and KNM-ER 3735 may belong to one species and larger specimens (eg. KNM-ER 1481, 1482, 3228) to another, the latter group being ancestral to *H. erectus.*

2.6.2 South Africa

The first fossil from South Africa assigned to the genus *Homo* was a mandible found at Swartkrans and thought by Broom and Robinson (1949b:322) to be "somewhat allied to Heidelberg man... and intermediate between one of the ape-men and true man" and who named it *Telanthropus capensis* (SK 15). Later another partial mandible (SK 45) was found (Broom and Robinson 1950) which was felt to be different from *P. crassidens* but was not assigned to *Telanthropus* until 1953 (Robinson 1953b). In 1961 Robinson reclassified *Telanthropus capensis* as *H. erectus.*

A couple of specimens previously assigned to *A. robustus* were found to belong to the same individual (SK 847) and called *Homo sp. indet.* (Clarke *et al.* 1970; Clarke and Howell 1972). In 1976 a new skull (STW 53) was discovered at Sterkfontein. Hughes and Tobias (1977:310) felt this was very similar to the early species of man originally described from Olduvai Gorge and designated *H. habilis.* Although there was some controversy over the presence of a second hominid at Swartkrans (eg. Wolpoff 1968, 1970 , 1971a, b) others (eg. Bilsborough 1971a; Clarke and Howell

1972) maintained that the presence of *Homo* at Swartkrans could not be disputed. The specimen SK 847 has been called *Homo* by some (Wallace 1978; Tobias 1980b) *H. habilis* by Howell (1978a), *H. erectus* by Clarke (1985), and even a gracile australopithecine (Olson 1978). Gutgesell (1970) re-examined Wolpoff's claims for a single species at Swartkrans which were based on stratigraphic and morphological evidence and concluded that *Telanthropus* was a separate species. Wolpoff (1970) refuted Gutgesell's arguments and maintained that the *Telanthropus* material represented small robust hominids. Most workers presently recognise the gracile material from Swartkrans and the non-*A. africanus* material from Sterkfontein as some form of early *Homo* – either *H. habilis* or *H. erectus.*

2.7 Phylogenetic Considerations

If *H. habilis* does indeed exist as a valid taxon there are a number of phylogenies in which it could be placed. As seen previously, Johanson and White (1978) see *A. afarensis* as the most recent common ancestor of *H. habilis* which in turn leads to *H. erectus* and *H. sapiens.* L.S.B. Leakey (1966) did not see *A. africanus* as the most recent common ancestor to *H. habilis.* Instead he believed that *Homo* extended further back in time (a belief supported for some time due to the early date for the KBS tuff at Koobi Fora). He also believed that a form of *H. habilis* led to *H. sapiens* and presumably that *H. erectus* was a side branch which became extinct. R.E.F. Leakey also believed that *Homo* extended further back in time and thought at one time (1972) that some of the South African material from Sterkfontein sampled early *Homo.* Many workers still place *A. africanus* as the most recent common ancestor of early *Homo* whether or not they recognise *H. habilis* and, indeed, evidence of African *H. erectus* seems to indicate that at least some of these early forms of *Homo* evolved into *H. erectus.* The question of whether or not these African *H. erectus* forms evolved into *H. sapiens* will be discussed in the next section.

2.8 Discussion

A number of workers have shown the affinities of the East African 'habilis' material to *A. africanus* and *H. erectus.* If *H. habilis* is a transitional form between these two species then this situation is to be expected. Evolution seems to progress in a mosaic fashion – a situation supported by various morphological features. In the dentition, for example, some workers would argue that there is little difference between *H. habilis* and *A. africanus* (eg. Robinson). Others (eg. Tobias 1980b) have pointed to the affinities between this material and *Homo.* Studies of the basicranium (Dean and Wood 1982) have shown specimens to have a mixture of features, some like *H.*

erectus and, suprisingly, like *A. robustus.* Other authors have argued that KNM-ER 1813 could not be placed in the same species as 1470 due to the extreme difference in cranial capacities. Finally, the new specimen from Olduvai, OH 62, shows postcranial similarities to *A. afarensis.* This mosaic of different features supports the idea of *H. habilis* as a transitional form but creates difficulties in assigning individual specimens and can also be used to support the idea of more than one species.

If more than one species of early *Homo* is being sampled, that is, that *Homo* was polyphyletic in its early stages (Bilsborough 1986), what criteria should be used to decide which specimens belong together and which are different? Should all australopithecine-like material be placed in the genus *Australopithecinae* and all erectus-like material in *Homo*? Should large forms be put in one group and small in another or earlier forms in one and later forms in another?

Some workers (eg. Howell 1978a, White *et al.* 1981, Tobias 1983) place all the gracile, non-erectus, forms in one taxon whose variability can be explained by sexual dimorphism, individual variation, and change over time. Others (eg. Stringer 1986) maintain that the variation in *H. habilis* exceeds that of extant primate species but different authors divide up the specimens in different ways depending on what criteria they use (see Groves and Mazak 1975). It is easy to say that the answer to the problem lies in a larger sample. However, using the present sample, one should ideally take into consideration as many metrical and morphological similarities and differences as is possible when trying to determine which specimens belong in which species.

There seem to be two major problems:

1. if *H. habilis* is a transitional form exhibiting mosaic evolution one cannot determine which characters began to change first; a problem made even more difficult due to the interrelatedness of cranial traits, where a change in one area has ramifications on all other areas to greater or lesser extent.
2. If early *Homo* was polyphyletic how does one determine the number of species existing at one time in any particular area?

The answer may not be obtainable at the present time (if ever) on the basis of the present fossil sample.

2.9 Homo erectus

2.9.1 Java

The first specimen of *H. erectus* was found in 1891 by Eugene Dubois and was first given the name of *Pithecanthropus erectus* based on a single calotte and femur. It was not until a quite a few years later that more discoveries of this species were found by von Koenigswald from 1936 to 1941, and later still by Jacob and Sartono in the 1960s and 1970s (Jacob 1973, 1975).

The stratigraphy of the Sangiran dome in Java has been divided into four units: 1) the Kalibeng Formation, dating to the Late Pliocene; 2) the Pucangan Formation, dating to the Early Pleistocene (Djetis fauna); 3) the Kabuh Formation, dating to the middle Pleistocene; and the Notopuro Formation, dating to the Late Pleistocene (Pope 1988). The lowest tuff of the Kalibeng Formation (Lower Tuff 1) has been dated by the fission track method to 2.99 ± .47 million years ago (mya). The Pucangan Formation is bracketed by the Lower Lahar at the bottom and the Grenzbank sediments at the top. Some of the Sangiran fossils are thought to originate from just below the Grenzank sediments but most are thought to be from the Kabuh Formation (and its equivalent at other sites in Java).

Fossil hominids have been found in other places in Central and Eastern Java: Trinil, Sambungmachen, Ngandong, Kedung Brubus, Sonde, and Mojokerto. The fossil level at Trinil has been correlated with Grenzbank-like sediments, that at Sonde is roughly equivalent to the Upper Kalibeng Formation, while that of Kedung Brubus has been correlated with the Lower Kabuh Formation. The dating of the remaining sites remains controversial either because their stratigraphy cannot be correlated with that at Sangiran or the provenience of the fossils is not known exactly.

The dating of much of the Sangiran stratigraphy is difficult because of problems in applying conventional dating methods. Pope (1988) presents an evaluation of the results of different methods used in the dating of the Javanese sites and attempts to date the earliest Javanese fossil hominids. Pope estimates that the earliest Javanese fossils are not older than 1.3 million years, a date based on comparative flourine content of some fossil specimens, and are likely to be less than .9 million years old. This author states that the Javanese fossil hominids are likely of Middle Pleistocene age, or very early Pleistocene, and they may span as little as .6 million years (Pope 1988).

For many years the Javanese fossil sample has not been thought to be homogeneous. Some specimens found in lower levels (ie. Djetis Beds, Sangiran) were felt to represent a more primitive hominid and were named *Homo modjokertensis* by von Koenigswald in 1936 (eg. S6) and later renamed *Pithecanthropus robustus* by Weidenreich in 1945. Other specimens include *Meganthropus paleojavanicus* and *P. dubius* which were thought to predate erectus forms and *P. soloensis* which post dates *H. erectus.*

The *Meganthropus* finds were thought to have affinities with *A. robustus* (S6). Robinson (1953a) claimed that *Meganthropus* resembled *P. crassidens* and placed it in the sub-family *Australopithecinae* along with the australopithecines from South Africa whereas *Pithecanthropus*, *Sinanthropus* (China), and later forms were placed in the sub-family *Euhomininae.* Von Koenigswald (1954) included *Pithecanthropus*, *Sinanthropus*, and *Meganthropus* in the subfamily *Pithecanthropi* which he believed gave rise to *H. sapiens.* In 1954 Robinson renamed *Meganthropus* as *Paranthropus paleojavanicus.* Remane (1954) criticised Robinson who defended his position (1955), but von Koenigswald (1957) rejected this renaming. Howell (1961) believed that *Meganthropus* was a late form of robust australopithecine while Le gros Clark (1964) claimed that the inclusion of *Meganthropus* in *H. erectus* would not make the range of variation greater than for modern *H. sapiens.* Tobias and von Koenigswald (1964) compared Bed I and II hominids from Olduvai Gorge with those from the Djetis Beds from Java and believed that *Meganthropus* was at the 'same level of hominization' as Bed I *H. habilis* which suggests a *H. habilis* stage of evolution in Java. Lovejoy (1970) examined the range of variation of P3, P4, M1, M3, and the profile through the mandibular symphysis and maintained that no morphological features of *Meganthropus* lay outside the range of variation for *H. erectus.* He believed that Bed II at Olduvai and the Djetis beds were probably contemporaneous and that a specific distinction of *Meganthropus* was not warranted. Howell (1978a) maintained that two grades of hominids existed in Java; that *Meganthropus* and the Modjokerto hominids were at least in part penecontemporaneous and may be 0.5 – 1.0 m.y. older than *H. erectus.* Orban-Segebarth and Procureur (1983) state that *Meganthropus* has marked australopithecoid traits in its dentition.

Jacob (1981) accepted three groups of Pithecanthropines in Indonesia:

1. *P. modjokertensis* from the lower Pleistocene in Sangiran and Perning;
2. *P. erectus* from the Middle Pleistocene from Sangiran, Trinil, and Kadung Brubus; and
3. *P. soloensis* from the Middle Pleistocene of Ngandong, Sambungmachen, and Sangiran and suggested that these three groups may be sub-species.

He believed *P. erectus* and *P. soloensis* evolved from *P. modjokertensis* but that possibly the erectus hominid evolved further anagenetically toward *H. sapiens.* Cybulski (1981) stated that there is increasing evidence that Solo man should be included in *H. erectus*, Santa Luca (1978) demonstrated the strong resemblance between Solo man and the Trinil zone *H. erectus*, and Holloway (1980) believed that Solo man was more closely related to the earlier Javanese *H. erectus* than to Neanderthals. J. de Vos (1985) supported a date for *H. modjokertensis* of less than 0.7 m.y. and believed that its morphology points to its belonging to *H. soloensis* whereas Bilsborough (1983) claimed that the Javanese material was from a single species that was variable and changed over time. Thorne and Wolpoff (1981) examined the case for regional continuity in Southeast Asia and maintained that Indonesian *H. erectus* is part of a morphological clade including later *H. sapiens* populations from Kow Swamp, Australia and that they are part of a chronospecies.

Franzen (1985) examined specimens of *P. dubius* (named by von Koenigswald in 1950 (S5) and later another specimen, S6, found in 1960 was included in this taxon) which he found to be more robust than *H. erectus* and more gracile than *Meganthropus*. He gave a date for the Djetis beds of 1.6 – 1.4 m.y. and suggested that the fossils from this time were either late australopithecines or early *H. erectus*.

2.9.2 China

A number of specimens have been found in China which have been attributed to *H. erectus*. The most important two sites are Zhoukoudian and Lantian. The first specimens were found at Zhoukoudian locality 1 which in 1927 were named *Sinanthropus pekinensis* by Davidson Black. These finds have been described in detail by Weidenreich but unfortunately the originals were lost during World War Two and only casts remain. Excavations continued after the War (eg. Woo 1956) and more material has since been found. The skulls have been compared to those found in Java but there is a greater range in cranial capacity. A few specimens have been found at two sites near Lantian where a skull cap and facial bones have been dated to approximately 700,000 years (Aiger and Laughlin 1973). The skull has been compared to the early *H. erectus* from the Djetis beds in Java with a cranial capacity of approximately 780 cubic centimetres and this is comparable to the earlier Javanese skulls. A mandible has also been found near Lantian and is approximately 300,000 years old. A number of individual teeth have been collected from Chinese drug stores which were later named *S. officinalis*. The hominid bearing sequence at Zhoukoudian has been dated using radiometric and paleomagnetic data to .5 to .23 million years whereas some of the Lantian hominids may be as old as the oldest known Javanese finds (Pope 1988).

A number of comparisons have been made between the Chinese and Javanese material. Weidenreich (1937a, b, 1938a, b) felt that *Pithecanthropus* and *Sinanthropus* were at the same general stage of evolution and that differences were due to regional or racial deviations. Von Koenigswald and Weidenreich (1938) in their announcement of a new *Pithecanthropus* skull found a number of similarities with the *Sinanthropus* material. In 1939 von Koenigswald and Weidenreich wrote a joint paper comparing the Javanese and Chinese fossils and concluded that differences were similar to racial differences found in modern man. Mayr (1944, 1950) concluded that Peking Man and Java Man were only subspecifically distinct and that all material could be placed into *H. erectus.*

2.9.3 East Africa

In 1960 a cranium (OH 9) was discovered at Olduvai Gorge near the top of Bed II and was referred to as *Homo* (Leakey 1961a). The cranial capacity was estimated to be 1067 cubic centimetres (Holloway 1973) and it was dated at approximately 1.1 m.y. Other specimens have been recovered from Bed IV (OH 12, 22, 28) and have been attributed to or compared with *H. erectus.* These later specimens have been dated to 0.83 – 0.62 m.y. (Rightmire 1984) and the cranial capacity of OH 12 has been estimated at 727 cubic centimetres. OH 9 has been called *H. erectus* by both Tobias (1965a) and Leakey (1966) among others. OH 13, previously referred to *H. habilis*, has been compared with a Javanese specimen (Tobias and von Koenigswald 1964) and Robinson (1965) has called this specimen *H. erectus.* Rightmire (1979) has compared the African specimens to those from China and found the African *H. erectus* to be more robust.

A number of specimens have been recovered from East Turkana that have been called or compared to *H. erectus.* Two crania, KNM-ER 3733 and 3883, have been called *H. erectus* by Leakey and Walker (1976), Walker and Leakey (1978), and Howell (1978a) with an estimated date of 1.3 – 1.6 m.y. A mandible, KNM-ER 992, was called *Homo* by Leakey and Wood (1973) and Wood (1976b) has compared specimens KNM-ER 992 and 730 to *H. erectus.* Groves and Mazak (1975) included KNM-ER 992 in a new species *H. ergaster* and Howell (1978a) has given the name *H. erectus* to KNM-ER 1501, 1502, 992, 1805, 1507, and 730. Leakey and Walker (1989) report a new partial skeleton (KNM-WT 15000) that they attribute to *H. erectus.*

Howell and Coppens (1976) have compared cranial fragments from Omo and Koobi Fora. These cranial fragments from Member K at Omo have been dated between 100 – 200,000 years and have been called *H. erectus* (Howell 1978b, Coppens

1978). A specimen from Bodo D'Ar, Ethiopia (Conroy *et al.* 1978) was considered to be less archaic than *H. erectus* from Asia or OH9 but more archaic than *H. sapiens* and thus is possibly a transitional form between *H. erectus* and *H. sapiens.*

A cranium from Lake Ndutu, Tanzania was called *H. erectus* (Clarke 1976) and dated between 0.6 – 0.4 m.y. but Stringer *et al.* (1979) consider this specimen to be a primitive form of *H. sapiens.*

2.9.4 South Africa

In 1949 a mandible was found at Swartkrans (SK 15) (Broom and Robinson 1949a) and was named *Telanthropus capensis.* Broom and Robinson (1949b, 1950) considered this specimen to be intermediate between apeman and true man while Tobias and von Koenigswald (1964) compared SK 15 with Sangiran B. Another specimen, SK 45, was described by Broom and Robinson in 1950 and differences in structure were noted between it and SK 15. Robinson (1953b) placed this specimen in *T. capensis* but in 1961 Robinson sank *Telanthropus capensis* into *H. erectus*; a position supported by Howell (1967).

In 1969 Clarke named SK 847, a composite cranium, *Homo* (Clarke, Howell, and Brain 1970). Clarke and Howell (1972) later stated that SK 847 was the same species as SK 15 and 45 but these specimens may have more affinities with *H. habilis* than *H. erectus.* Olson (1978) calls the Telanthropus material *H. erectus* but includes SK 847 in *H. africanus.* He states that *H. erectus* in South Africa is 500,000 years old or less and that SK 847 dates between 1.5 – 2.0 m.y. Walker (1981) called SK 847 a very old adult *H. erectus* similar to KNM-ER 3733 and Clarke (1985) now calls this specimen *H. erectus.*

2.9.5 North Africa

In 1933 a partial mandible and broken maxilla were found in Morocco in a quarry near Rabat and are thought to be at least 200,000 years old. In 1954-55 in Algeria three mandibles and a partial cranium were found at Ternifine dating to 500 – 700,000 years and were named *Atlanthropus mauritanicus* (Arambourg 1955) and in 1954 in Morocco two mandibles were found at Sidi Abderrahamen dating to 200,000+ years. Arambourg and Biberson (1956) included these specimens plus the Rabat mandible in *A. mauritanicus.* In 1958 a mandible was found at Temara, Morocco dating to about 200,000 years. At Thomas Quarry in Morocco a mandible was found in 1969 dating to c. 350,000 and in 1972 a face and cranial bones were found dating to c. 200,000 years. In 1971 a skull approximately 200,000 years old was found at Salé, Morocco (Jaegar 1975).

Howell (1960) noted the close resemblance in teeth and jaws of the Ternifine material to Asian *H. erectus.* Jaegar (1975) (cf. Cybulski 1981) grouped later specimens from Morocco, Sidi Abderrahamen, Rabat, and Salé as *H. erectus* but noted some modern features. Howell (1978a) groups Rabat, Sidi Abderrahamen, Salé, Thomas I, and Ternifine specimens as *H. erectus* but notes some transitional features.

2.9.6 Europe

In 1907 the Mauer mandible was found near Heidelberg, Germany, dating to 0.5 m.y., and was called *H. erectus* since it was thought to be contemporaneous with Asian and African *H. erectus.* Howell (1960) considers this specimen to be distinct. A mandible was found in Montmaurin, France which Vallois (1956) found to have a number of Neanderthal features but also some like the Mauer mandible. In 1960 a skull was found in Petralona, Greece and dated to 300,000+ years. Stringer (1974) described its morphology as being intermediate between *H. erectus* and the Neanderthals. Stringer, Howell, and Melentis (1979) emphasise this specimen's archaic and sapient features and Rightmire (1985) agrees that this specimen is an early form of *H. sapiens.* In 1965 a single tooth and an occipital were recovered from Vertesszöllös which Wolpoff (1971c, d, 1977) considered to be *H. erectus* but Thoma (1981) found the morphology to be intermediate between *H. erectus* and *H. sapiens* and would call them *H. sapiens* on phylogenetic grounds. A face, two mandibles, and some teeth were recovered from Arago Cave, France between 1969 and 1971 and were dated between 275 - 300,000 years. Brace and Montagu (1977) state that these specimens are *H. erectus* but Rightmire (1985) found them to be unlike African and Asian *H. erectus.* Cranial fragments from Bilzingsleben, Germany were compared by Vlcek (1978) to OH9, Sangiran 17, and Sinanthropus 3. Vlcek and also Mania and Vlcek (1981) consider this specimen to be a geographical variant of *H. erectus* and named it *H. erectus bilzingslebensis.*

2.10 Phylogenetic Considerations

A number of authors have attempted to provide a definition of *H. erectus* and determine which fossils can be included in their diagnosis. Although many of the European specimens possess characters which could link them to *H. erectus* there are a number of authors who would argue against their inclusion in this species. Howell (1960) stated that there is no evidence of *Pithecanthropus* in Europe and saw specimens like Mauer, Vertesszöllös, and Petralona as transitional forms between *H. erectus* and *H. sapiens* (1978a) while Jelineck (1980) called all middle and late Pleistocene hominids from Europe *H. sapiens.* Howell (1981) stated that there were a number of characters which defined *H. erectus* and since the European specimens did not fit this definition they were not *H. erectus* while Wood (1984) maintained that the *H. erectus* affinities of the European specimens had not been demonstrated. Thus the European fossils may represent transitional forms linking *H. erectus* with archaic *H. sapiens.*

Several authors exclude European fossils from their assessment of *H. erectus.* Wood (1984) maintained that fossils from Zhoukoudian and Sangiran form the hypodigm of *H. erectus* but that there is a resemblance between African and Asian specimens. Wood used a 'combination' definition of *H. erectus* and since KNM-ER 3733 and 3883 from Koobi Fora lack some autapomorphic features of *H. erectus* they could not be included in this species. If the definition was widened to include them then *H. erectus* would not possess any autapomorphies, that is, it would lack features which in combination distinguish it from *H. habilis* and *H. sapiens* and would diminish the differences between *H. habilis* and *H. erectus* to trivial ones. Andrews (1984) stated that the majority of characters used to define *H. erectus* were primitive retentions, only a few of which are diagnostic of the species and most of these characters are not present in African *H. erectus.* He maintained that Asian *H. erectus* show a unique set of derived traits, and that any shared traits between Asian and African forms are primitive ones (except an increase in brain size), therefore there are no grounds for combining the two groups. The African sample retains some primitive features for which *H. erectus* is derived and so are similar to *H. habilis* and other non-erectus forms. Stringer (1984) would classify the Asian hominids into *H. erectus sensu stricto* and shows that the similarities between Asian and African forms are due to shared primitive traits. He suggests that if the African specimens formed an early *H. erectus* grade, then the difference in characters in the Asian forms may indicate divergence from the primitive pattern. Stringer argues that a widely-defined definition of *H. erectus* can be justified phenetically to encompass variation but not cladistically, as this obscures the distinction between *H. erectus* and *H. sapiens.* He supports a grade definition of *H. erectus* consisting of general features thus the early African fossils are primitive members of a grade which do not possess the specialised characteristics of the later Asian specimens. Bilsborough and Wood (1986) include African and Asian specimens in groups of early and late *H. erectus.* Thus *H. erectus* may be restricted to Asia or, if a wider definition is adopted, include the African specimens.

There is some debate in the literature concerning the origin and fate of *H. erectus.* Bilsborough and Wood (1986) claim that there is a distinct break between non-erectus forms and early African *H. erectus* and argue for an African origin of this species. Stringer (1984) argues that the Asian hominids had already separated from a common ancestor possessing derived characteristics which were distinct from the Koobi Fora hominids. Bilsborough (1983) argues that *H. erectus* is a well-defined chronospecies and maintains that in East Africa, the change from early *Homo* to *H. erectus* "...does not require any rapid or dramatic evolutionary mechanism".

Concerning the relationship between *H. erectus* and *H. sapiens* two scenarios emerge from the literature. Andrews (1984) provides two alternatives:

1. if *H. habilis* evolved into *H. sapiens* then the erectus-like characters found in *H. sapiens* evolved in parallel; or
2. if *H. erectus* evolved into *H. sapiens* then an evolutionary reversal occurred where the derived characters in *H. erectus* reversed in *H. sapiens* to look like the primitive traits found in *H. habilis.*

He argues that the first alternative is more parsimonious; that the African specimens were close to a line leading to *H. sapiens* and that Asian *H. erectus* was somehow removed from this lineage. This idea was first put forward by Leakey (1966) who argued that *H. habilis* evolved into *H. sapiens.* Wood (Bilsborough and Wood 1986) agrees with Andrews that cladistically, *H. habilis* has equal or greater claim as the sister group of *H. sapiens* whereas Stringer (1984) believes that Asian *H. erectus* was excluded from the ancestry of *H. sapiens.* Bilsborough and Wood (1986) believe that phenetically, there is a relatively small distance between *H. erectus* and *H. sapiens* and Bilsborough supports the idea of continuity between *H. erectus* and *H. sapiens.*

2.11 Discussion

H. erectus appears in the fossil record as a single species which is geographically and locally variable and which exists from approximately 1.6 to 0.4 m.y. Some definitions of *H. erectus* include only specimens from Asia while others include the African specimens. Specimens from Europe are excluded from many definitions of *H. erectus* since they may well be transitional forms between *H. erectus* and *H. sapiens* and many workers would include them in *H. sapiens* on phenetic and cladistic grounds. A number of workers support an African origin of *H. erectus* but there is debate over the relationship of *H. erectus* and *H. sapiens.* One phylogeny would see early forms of *Homo* in Africa evolving into *H. sapiens.* Another sees the origin of *H. erectus* in Africa which either evolved through Asian *H. erectus* to *H. sapiens* or else the Asian forms were removed from an ancestral role and the African *H. erectus* evolved into *H. sapiens.*

CHAPTER 3: METHODOLOGICAL CONSIDERATIONS

3.1 Introduction

This chapter involves a brief review of techniques used in this study. The first section of the chapter outlines the univariate and multivariate statistical methods used in this thesis. In the second section I present a brief discussion of cladistic principles, as well as a review and critique of previous studies of the hominids and hominoids.

3.2 Statistics

3.2.1 Introduction

Fossil hominids have been described in both qualitative and quantitative terms using metric and non-metric traits. Non-metric traits have been used both in the definition of fossil species (eg. Leakey *et al.* 1964) and in analyses of phylogenetic relationships between fossil hominids (eg. Skelton *et al.* 1986). One of the main disadvantages of such traits is that they are subjective. For example, what one worker would record as "large", another (or the same worker at different times) may record as "intermediate" in size. This makes it difficult to measure the range of variation in such traits.

Metric traits, on the other hand, are measurable and while subject to inter- and intra-observer error are so to a lesser degree than non-metric traits. Finally, metric traits are a useful means of summarising information and can be used in univariate and multivariate morphometric analyses. I have chosen, therefore, to use metric traits in an attempt to measure within and between species variation in modern hominoids to determine the degree of sexual dimorphism and the pattern of variation in the extant species for use as models to: 1) test the homogeneity of the fossil hominid species; and 2) discriminate between species of fossil hominids.

A number of workers have used metric data in the taxonomic allocation of individual fossils (eg. Wood and Van Noten 1986; Wood and Abbott 1983) as well as to discriminate between species of fossils (Chamberlain 1987; Stringer 1986; Bilsborough 1984; Kimbel *et al.* 1984; Johanson and White 1979). Other workers have examined within species variation in an attempt to determine the degree of sexual dimorphism in fossil hominids. These authors have used the knowledge of sexual dimorphism in modern hominoids (eg. Wood 1976a) as a yardstick against which to assess dimorphism in fossil hominids (eg. Lieberman *et al.* 1988; Chamberlain and Wood 1985; Wood 1985; Wolpoff 1976). Thus metric traits have been used to make quantitative comparisons between different specimens and between different species.

3.2.2 Univariate Analysis

Some studies have used univariate methods in the analysis of fossil hominids (eg. Kimbel and White 1988; White 1985). Univariate methods are one appropriate way of analysing within and between species variability in the fossil hominids because of the fragmentary nature of the material. The majority of discussion about the gross morphology of fossil hominid species tends to revolve around the more complete crania and mandibles. However, to assess the total range of variation of the hominid sample one must include any and all material available. Thus a fragment of a mandible, for example, may provide only one or two measurements which may preclude its inclusion in any multivariate analysis, but which may yield useful information about within or between species variability. According to Chamberlain (1987:87) "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... or in the analysis of hominid dental metrics...".

In the Univariate Analysis of this study, I decided to follow the example of Wood (1976a) to calculate the sample statistics of the mean, standard deviation, and standard error; the F value and T value which are tests of significance between two samples; the Coefficient of Variation (CV); and percentage sexual dimorphism. These statistics can be used to examine the total range of variation within the modern hominoids (thus providing a measure of homogeneity within groups) as well as to determine if a common pattern of sexual dimorphism exists with which to assess sexual dimorphism in the fossil hominids. Because the degree and pattern of sexual dimorphism within the fossil hominids is unknown, the only sample statistics that can be used to summarise their data are the mean, standard deviation, and the CV of each fossil hominid sample.

The F test investigates whether the sample variances of the two sexes are sufficiently alike to warrant the assumption that they are independent estimates of the same population variance while the t test examines the significance of the difference between the means and assumes that the means and variances of the parent populations are identical. The pooled estimate of variance is used because of small sample numbers. Theoretically, if a significant difference between the variances occurs between the sexes for any variable, their variances should not be pooled to derive a common variance for the basis of the t test. These characters, however, may be of functional importance and therefore their variances will be pooled and included in the following analyses.

The CV allows the comparison of samples whose values differ in absolute size since it is independent of any unit of measurement if the variables are homologous or if they all belong to the same category (ie. linear dimensions). Simpson, Roe, and Lewontin (1960) maintain that most values of CV for a single species should lie between 4 and 10 per cent with an average value of 5 or 6. Groups with a value of CV greater than 10 per cent are probably impure with an underlying distribution containing unrecognised subcategories which may be due to the inclusion in the sample of individuals of different age or inclusion of individuals from different taxonomic categories.

A problem arises in fossil samples where it is impossible to guarantee a homologous sample, that is, samples cannot be divided by sex, geological age, or taxon. Thus the value of CV in these samples can be higher, in general, than in a carefully selected sample of extant individuals. Simpson, Roe, and Lewontin (1960) recommend that when making taxonomic comparisons of fossil samples it is better to select characters with relatively little variability than those which are highly variable, since a highly variable character is a reflection of intra-specific variability and is not as reliable to check taxonomic differences. According to Thomas (1976:83) "There is an apparent trend in evolution for adaptive characteristics to exhibit less variability than nonadaptive traits" and Wolpoff (1969) thinks that the most stable traits are ones on which selection is acting with the strongest intensity.

Variables with high values of CV may reflect sexual or even species differences and so in order to determine the homogeneity of a fossil sample it is necessary to find variables which are not dimorphic or variable for the modern species. If the values of CV for the fossils are considerably greater than those for the modern groups for these variables then differences within the group may be due to reasons other than sexual dimorphism.

Sokal and Rohlf (1981) suggest the use of confidence limits as a test for comparing CV's. They use the formula CV ± the standard error of the CV multiplied by the t value (p=0.5 for a 2-tailed test using n-1 degrees of freedom). This gives the 95 % confidence limits of the CV. Confidence limits will be used in the comparison of fossil hominid with extant hominoids whenever a major difference occurs between their values of CV for any particular character (see Chapter 5).

The Univariate Analyses of within- and between-species variation of the extant hominoids and fossil hominids is presented in Chapter 5.

3.2.3 Multivariate Analyses

Multivariate analyses are valuable when comparing the relationships within and between groups. They can be used to compare the range of variability of two or more species and their separation. Multivariate analyses have the advantage over univariate methods in that they can assess a combination of variables at the same time which can result in the simple description and understanding of complex phenomena (Reyment *et al.* 1984).

The majority of metric analyses of the fossil hominids have involved the use of multivariate statistical methods using continuous linear or angular measurements. Some workers transform their data to remove size as a variable while some do not. Chamberlain (1987) suggests that morphometric comparisons between hominids may be influenced by size effects. Size differences between specimens, however, are a large component of sexual dimorphism and therefore in an analysis of within species variability, it may be desirable to retain the size component. Also, there are ways of examining the differences between individuals and species without resorting to data transformation. For instance, in Principal Components Analysis and Canonical Variates analysis, the first axis is often largely a size component or variate while the remaining components and variates are often a representation of shape variation (Reyment *et al.* 1984:22).

Chamberlain (1987) lists over 40 multivariate studies of data from fossil hominids. The main multivariate techniques used are Cluster Analysis, Principal Components Analysis, Canonical Variates Analysis, and Mahalanobis Distance (generalised statistical distance). Cluster Analysis is used to identify relatively homogeneous groups of cases based on selected variables. It computes measures of the similarity or distance between all cases. Based on these, similar cases are grouped into clusters, using one of several criteria for cluster formation, and the clusters form a hierarchy of similar groups. In this way groups of cases can be determined as well as the characters they share with, and in which they differ from, one another (Norusis 1988). Among those that have used the Cluster technique in the analysis of the fossil hominids are Chamberlain (1987), Corruccini and McHenry (1980), and McHenry and Corruccini (1978).

Principal Components Analysis (PCA) results in the collapsing of a set of intercorrelated variables onto a smaller number of "composite" variables. In other word, PCA classifies variables to see which ones best discriminate between cases. PCA makes linear combinations (PC's) of the observed variables where the first PC accounts for the largest amount of variance in the sample, the second PC, the next largest amount of variance uncorrelated with the first PC, and so on. It does this by maximising the resulting scores of each linear combination such that similar individuals will be located close together and dissimilar individuals will be "forced" apart (Norusis 1988; Reyment *et al.* 1984; Sokal and Rohlf 1981). Examples of studies of fossil hominids that have utilised PCA include O'Higgins (1989) in an analysis of cranial variation, Bräuer and Leakey (1986) in the analysis of the vault, and Read (1984) who examined teeth.

Canonical Variates Analysis (CVA) is used to establish which characters are most important for distinguishing between groups. Based on a set of known groups, linear combinations of the variables are formed that best separate the groups. The accuracy of the classification can then be assessed by applying the model to cases whose group membership is known and compare the predicted to the actual group membership. It can also be used as a model to classify "unknown" specimens to known groups (Norusis 1988; Reyment *et al.* 1984; Sokal and Rohlf 1981). CVA has been used by numerous workers to determine which extant primate species the fossil hominids most resemble morphologically (eg. O'Higgins 1989; Van Vark 1984; Bilsborough 1984; Kennedy 1983; Clark 1980; Susman and Creel 1979).

The generalised statistical distance (D^2) of Mahalanobis can be used to determine how far two populations are separated. Generalised distances can be calculated between all pairs of populations and may help to illuminate major sources of variation. D^2 can be used in conjunction with CVA to determine how far populations are separated by any one CV. This technique has been used by a few workers in the analysis of the fossil hominids including O'Higgins (1989); Kennedy (1983, 1984); Bilsborough (1984); Corruccini and McHenry (1980).

3.2.4 Discussion

Within-species variation

PCA and Cluster Analysis are similar in that they can both be used to identify fossil groups. PCA seems to have an advantage over Cluster Analysis in that it determines which variables are acting to group specimens together. Thus PCA will more appropriatly meet the aims of this thesis than Cluster Analysis since the former: 1) seeks to determine the major sources of variation in the data; 2) it establishes which characters are important for distinguishing between individuals; and 3) relationships between individuals can be examined in two or more dimensions. I therefore chose to use PCA in the multivariate analysis of within species variability. A more detailed discussion of this technique can be found in Chapter 4.

Between-species variation

CVA is a more direct approach than D^2 to determine sources of variation between species. According to Reyment *et al.* (1984:17) "This technique has the advantage that, should the arrangement of the populations require three or more dimensions for its proper expression, the canonical variates can be taken two at a time so that different aspects of the relationships can be examined in detail" and these aspects can be displayed in two or more dimensions. CVA is a valuable tool when dealing with many populations (or samples) since it provides a simple representation of the group relationships in multidimensional space and "the problem of unravelling relationships for a large number of generalized distances can quickly become formidable" (Reyment *et al.* 1984:17). Thus I chose to use CVA in the analysis of between-species variability. A more detailed description of the Canonical Variate technique can be found in Chapter 4.

3.3 Hominoid Systematics

3.3.1 Introduction

The reconstruction of phylogenetic history involves determining the pattern of descent of a group of organisms from their common ancestor. There are a number of approaches to reconstructing phylogenies but the method to be used in this study is known as cladistics (Mayr 1965) or phylogenetic systematics (Hennig 1950, 1965). In this study the cladistic approach is used as a method of estimating the pattern of descent of organisms from their common ancestor rather than in a classificatory sense (Mayr 1974).

Cladistics is a method of biological classification where organisms are ranked on the basis of their recency of common descent and which seeks to identify sister groups, that is taxa, or sets of taxa, that are more closely related to each other than to other taxa. The definition of a species relies on derived features. In Cladistics, characters of morphological resemblance between organisms are divided into ancestral/primitive, derived, or convergent features. Primitive features are those characters inherited from distant ancestors (plesiomorphic), derived characters from a more recent common ancestor (apomorphic), and convergent characters are those that have occurred independently in separate lineages. It is the derived characters which are used as evidence of relationship, where the relationship between groups of organisms is dependent on shared derived features (synapomorphies) and membership within a group is dependent on unique derived features (autapomorphies). The shared derived features are used to construct branching patterns of phylogeny. Synapomorphies are used to form cladograms in which nested sets of features are depicted in hierarchical form and where synapomorphies can be shared by two or more taxa. Once taxa are defined on the basis of unique derived features they are placed on the terminal branches of the cladogram and their relationship with other taxa are depicted in the branching structure. Cladists also construct classifications based on these branching patterns, a practice that has received widespread criticism (Mayr 1974; Van Valen 1978; Gingerich 1979b; Bretsky 1979).

3.3.2 Other Methods

The cladistic approach is not the only method used to determine relationships between organisms. Other methods include Phenetics (Sokal and Sneath 1963; Sneath and Sokal 1973), Evolutionary Systematics (Simpson 1961, 1975; Mayr 1969, 1974) and Stratophenetics (Gingerich 1977, 1979b, 1985; Gingerich and Schoeninger 1977). With Phenetics, organisms are classified on the basis of 'overall' similarity and similarity is assessed by the presence or absence, size, shape, or position of many unweighted features (Sokal and Sneath 1963). Evolutionary Systematics classifies and ranks organisms on the basis of phylogenetic branching and on the amount and nature of evolutionary change between branching points with some characters weighted as more or less useful. The Stratophenetic approach evaluates phenetic resemblances of fossils within their stratographic context (Gingerich and Schoeninger 1977) (See Delson, Eldredge and Tattersall 1977 for a criticism of this approach).

The methods used in all these approaches, and criticisms of each, are outlined in a multitude of articles, notably Delson (1977), Tattersall and Eldredge (1977), Eldredge (1979), Cracraft (1979), Eldredge and Cracraft (1980), Arnold (1981), Tassy (1981), Tattersall (1982), and Patterson (1982). A plethora of arguments have been made over the years as to which method should be used for phylogenetic reconstruction and classification, though Mayr (1981) points out the advantages of using the best parts of each method. Some authors (eg. Tattersall and Eldredge 1977) recommend using cladograms as the basis for phylogenetic trees and phylogenetic trees as a basis of postulating a scenario (utilising information regarding culture, adaptation, ecology, and environment). If one is interested in determining the closeness of relationships between groups by reason of common ancestry then cladistics emerges as the best method (see Trinkaus 1990 for a discussion of the advantages of cladistics but also of its limitations).

3.3.3 Polarity

One of the problems of cladistics is the determination of the sequence of change (or polarity) of primitive/derived characters. Some authors recommend the use of ontogenetic data to aid in reconstructing phylogeny (eg. Bonde 1984; Eldredge and Novacek 1985), and some functional considerations (Delson 1977), as well as the traditional use of outgroup comparison (eg. Eldredge and Cracraft 1980). Outgroups are usually the closest relations of the taxa being examined (though taxa of more remote relationships can be used) to estimate polarity sequences. Their use does, of course, presuppose some knowledge of the phylogeny under consideration, at least in its broad outlines.

3.3.4 Convergent and Parallel Features

Another criticism of cladistics is its inability to deal with convergent or parallel characteristics. Arnold (1981) argues that cladists acknowledge the problem of parallelism and convergence but argue that this problem can be resolved by accepting relationships supported by the greatest number of derived features. According to Skelton, McHenry, and Drawhorn (1984) this problem is resolved by using the principle of maximum parsimony where the 'best' cladogram requires the fewest evolutionary events (acquisitions, losses, or modifications of traits) and so allows tenable hypotheses to be made about evolutionary relationships. This method penalises hypotheses which require evolutionary reversals and convergences.

3.3.5 Evolutionary Rates

Another set of arguments affecting cladistic analyses of hominids concerns the speed and means of evolution. Two main camps exist: those who uphold phyletic gradualism and those who support a punctuated equilibria model. A phyletic gradualist regards change over time within lineages as a significant source of evolutionary differences leading to arbitrary chronospecies (segments of a lineage). Thus these workers recognise anagenetic evolution (change within a lineage without speciation) and give it a major role in evolution (Bilsborough 1983:162).

In 1972, Eldredge and Gould proposed that evolution or change occurs in very rapid events of speciation. During the lifetime of a species little change occurs (stasis) or else morphology fluctuates very little about a stable mean. A period of stasis may then be followed by rapid change associated with speciation. These speciation events usually involve small isolated populations close to the limit of a species range (allopatric speciation). Gould and Eldredge (1977:120) maintain that "...major morphological evolution must occur by repeated, rapid speciation since too little time is available for change by standard, gradualistic rates".

A number of workers (Gould and Eldredge 1977; Eldredge and Tattersall 1982; Stanley 1979, 1982) regard the hominid fossil record as a good example of punctuated equilibrium. Cronin *et al.* (1981) maintain that a more parsimonious explanation is one of phyletic gradualism while a number of other authors argue both for and against these theories (eg. Pichardo 1978; Ginzburg 1981; Hoffman 1981; Lemen and Freeman 1981; Schopf 1981).

One of the main pieces of evidence used by punctuated equilibria proponents is *H. erectus* (Gould and Eldredge 1977; Rightmire 1981). Eldredge and Tattersall (1982) state that this species lasts at least a million years with virtually no change. They state that local and geographical differences are as striking as the differences between early and late specimens but despite these differences *H. erectus* is "...an instantly recognizable gestalt" and this is evidence of stasis (1982:144-145).

Rightmire (1981) examines the pattern of distribution of four characters to see if they show significant change: cranial capacity; width of cranium at cranial base; dimensions of the second permanent molar; and the robusticity of the mandible. Apart from a slight trend for increase in cranial capacity there was no evidence for change in the other characters. The main criticisms of Rightmire's data are that: 1. he does not establish that *H. erectus* is more stable than other taxa; and 2. his characters are ones used to define the species and therefore should not change and thus are not evidence for stasis (see also Rightmire 1984, 1985, 1986; Wolpoff 1984, 1986).

Delson (1981) presents evidence for speciation in Europe. He suggests that *H. sapiens* may have evolved there first due to isolation caused by glaciation, that is *H. sapiens* evolved once in isolation rather than gradually in many places.

Bilsborough and Wood (1986) show that diversity exists among the *H. erectus* specimens and that change occurs between early and late specimens. Stringer (1984) maintains that the differences between the African and Asian specimens contradicts claims for stasis. Despite this problem of determining the extent of change versus stasis, some of the earliest *H. sapiens* show mosaic features that are erectus-like. Bilsborough and Wood (1986) feel that these similarities demonstrate the continuity of the fossil record.

Discussion

The hominid fossil record is thought to be a good example of both phyletic gradualism and punctuated equilibrium, but this depends on how the evidence is interpreted. A phyletic gradualist can demonstrate that change occurred over time and that continuities exist between ancestor and descendent species. A punctuated equilibrium supporter sees no continuities between hominid species. Instead, they see periods of stasis followed by sudden change. Bilsborough (1983) maintains that the hominid fossil record is too meagre and the material too contentious to determine the validity of either model; that both models rely on small samples which in some cases are insecurely dated. Instead, he believes that the earlier stages of hominid evolution are polyphyletic with indications of speciation events. This, however, does not validate the punctuated equilibrium model as the gradualists also allow for change through speciation events. Since the hominid fossil record does not fully document gradual or episodic change perhaps it is best to side with Cronin *et al.* (1981:121) for the time being who believe that the evidence of the fossil hominids is "...still most reasonably interpreted by a model of phyletic gradualism with varying rates" (see also Tobias 1985).

The implications for cladistics are related to the interpretation of the cladogram. If evolution were solely anagenetic, change within a lineage, then the nodes in the cladogram reflect this change, that is, the acquisition of new features. On the other hand, if evolution was periodic, then the nodes represent speciation events. Since it is likely that evolution occurred both anagenetically and periodically, or a combination of the two, there is no way of distinguishing between any combination of these two processes. For the purposes of this study, however, the nodes of the cladogram represent the acquisition of new features. The internal nodes of the cladogram are defined by changes in character states (synapomorphies) where changes at any one node are the differences between its character states and those at the preceeding node. These character states are used to identify and define sister groups (see section 7.2.1 for further details).

3.3.6 Previous Cladistic Studies of the Hominids

The phylogenetic reconstruction of the hominid lineage has a long history (Brace 1981) but a cladistic approach to hominid phylogeny was only introduced relatively recently. Eldredge and Tattersall (1975) published the first cladistic analysis of the Hominidae (see figure 3.01) incorporating *H. habilis* in *A. africanus* and *A. boisei* and *A. robustus* in *Paranthropus*. They placed *A. africanus* as the sister taxon of *Paranthropus* and *Homo* because of the primitive nature of *A. africanus* rather than the presence of symplesiomorphic characters in *Paranthropus* and *Homo.*

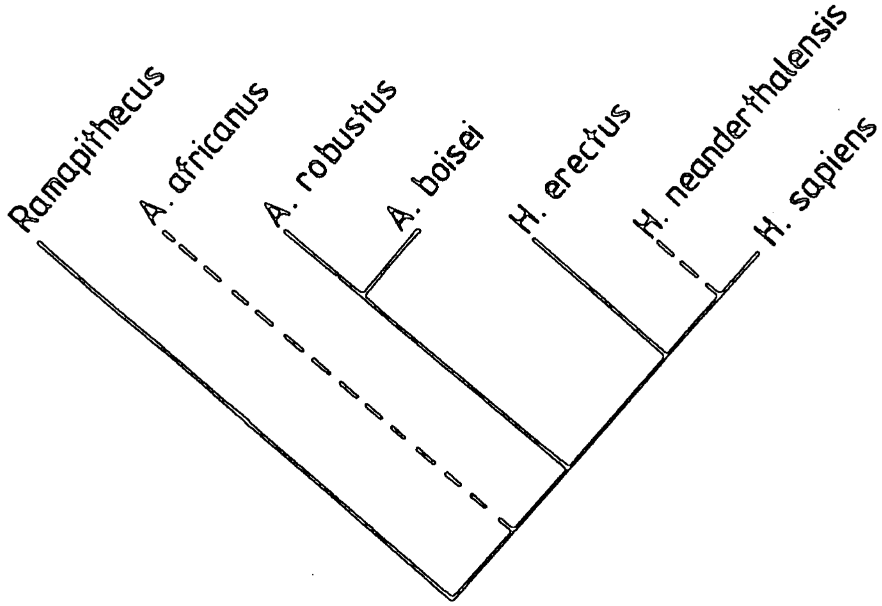


Figure 3.01 Cladogram from Eldredge and Tattersall (1975)

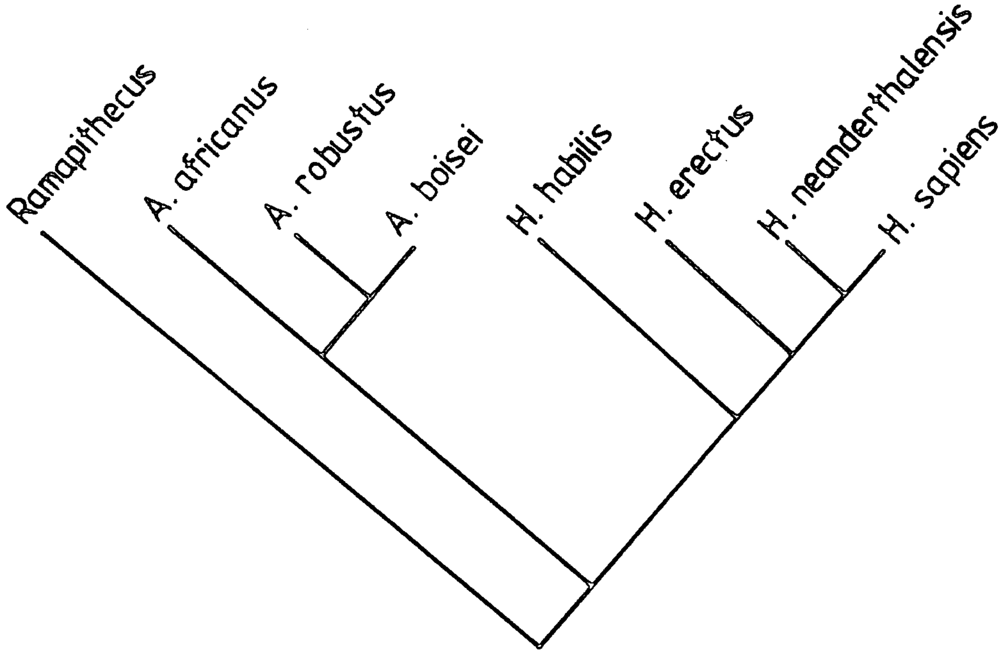


Figure 3.02 Cladogram from Tattersall and Eldredge (1977)

Delson *et al.* (1977), in order to resolve the trichotomy between *A. africanus*, *Paranthropus*, and *Homo*, included an examination of postcranial characters along with those used by Eldredge and Tattersall (1975) and inferred some synapomorphies between *A. africanus* and *Homo* due to their relative femur lengths. But subsequent to this paper Tattersall and Eldredge (1977) reassessed the postcranial morphology and found that australopithecines showed a derived form of femur head and length not shared with *Homo* and represented all australopithecines as a sister taxon of the genus *Homo* (see figure 3.02).

Olson (1978) included *A. africanus*, *H. habilis*, and early *Homo* material from Swartkrans into a taxon he called *Homo africanus* while *A. robustus* and *A. boisei* were placed into the genus *Paranthropus* and he presented a cladogram similar to that of Delson *et al.* (1977).

In 1979 Johanson and White, on the basis of the recently discovered Hadar material, constructed a cladogram which placed *A. afarensis* as the sister taxon of the other hominids with *A. robustus* (*A. robustus + boisei*) and *A. africanus* as sister taxa (see figure 3.03). Later White *et al.* (1981) corrected this cladogram and placed all australopithecines as sister taxa to the other hominids (see figure 3.04) (They stated that the cladogram in Johanson and White (1979) contained an error in its second branch). They described a number of derived characters in the mandible, teeth, and face shared by *A. africanus* and *A. robustus* but not those supporting the placement of the other hominids.

Corruccini and McHenry (1980) criticised the cladistic analyses of Eldredge and Tattersall (1975), Delson (1977), and Delson *et al.* (1977) because they did not clearly define the characters used or demonstrate their morphoclinal variation. Corruccini and McHenry used a number of metric traits, the majority being dental ones, and their cladogram was similar to that of White *et al.* (1981) (see figure 3.05).

Olson (1981) examined cranial traits in *A. afarensis* and rejected the idea that the size variation in the sample was the result of sexual dimorphism. He divided the material into two groups, one having affinities with the robust australopithecines and the other with the gracile hominids, *A. africanus* and *Homo.* In another paper Olson (1985) maintained this viewpoint.

Kimbel *et al.* (1984) provided a list of shared derived characters in hominids and present four different cladograms: 1. *Homo*, *A. africanus*, and the robust australopithecines as a sister group to *A. afarensis*; 2. *A. africanus* and the robust australopithecines as a sister group to the other hominids; 3. *A. afarensis* and the

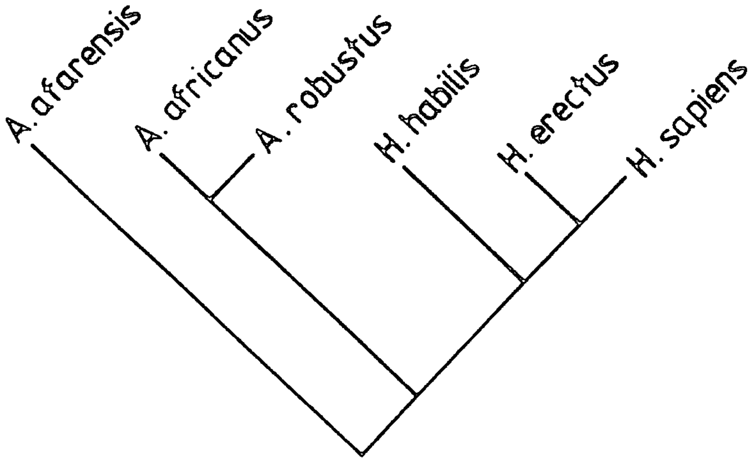


Figure 3.03 Cladogram from Johanson and White (1979)

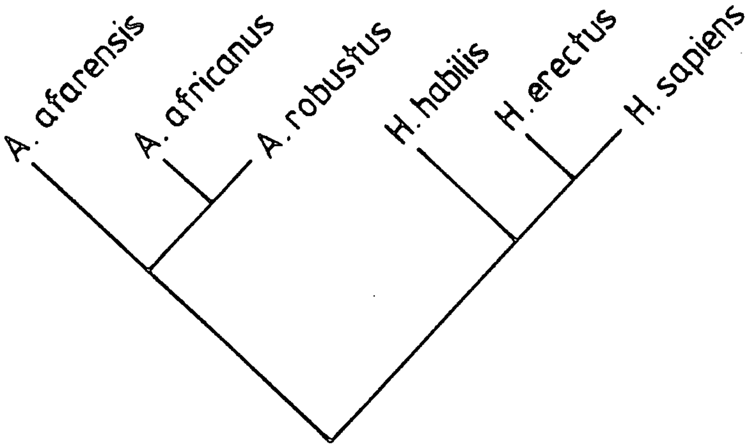


Figure 3.04 Cladogram from White et al. (1981)

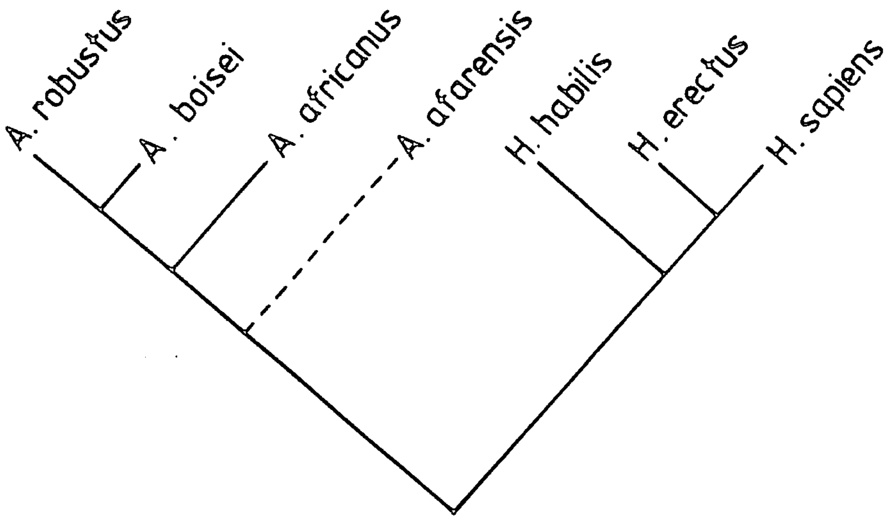


Figure 3.05 Cladogram from Corruccini and McHenry (1980)

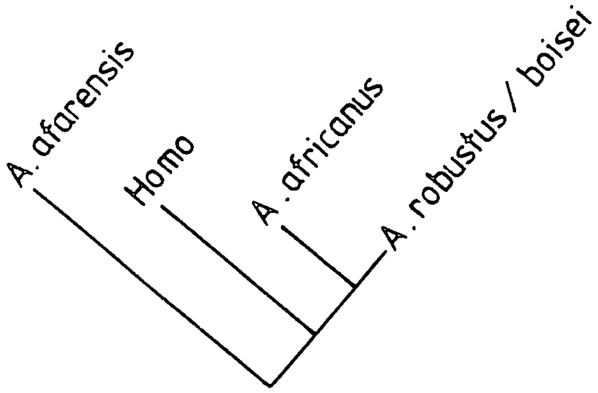


Figure 3.06 Most parsimonious cladogram of Kimbel et al. (1984)

robust hominids as sister group to the other hominids; and 4. *Homo* and the robust hominids as sister group to the other hominids. These authors favoured the second proposal though the first one was the most parsimonious arrangement of the data (see figure 3.06).

Skelton *et al.* (1984) performed a cladistic analysis to determine the relationships between the australopithecines and *H. habilis* using 69 traits from various sources in the literature and they divided the traits into twelve complexes. In the most parsimonious cladogram, supported by 45/69 traits, *H. habilis* and *A. robustus + boisei* were more closely related to each other and were more likely to be a sister group to *A. africanus* than were *A. africanus* and *A. afarensis* forming a sister group (see figure 3.07). They concluded from this cladogram that the last common ancestor of the robust hominids and *H. habilis* postdated *A. africanus.* Other authors have noted a resemblance between the robust hominids and *H. habilis* including Dean and Wood (1981, 1982), Wolpoff (1978), and Wood (1981) though Kimbel *et al.* (1984) provided convincing arguments why these traits would have evolved in parallel. Skelton *et al.* suggested a phylogeny where *A. afarensis* was ancestral to *A. africanus* which in turn was ancestral to the robust australopithecines and to *H. habilis.*

Wood and Chamberlain (1986) used measurements of cranial characters in a cladistic analysis of the australopithecines and *Homo* and presented a cladogram in which *A. afarensis* shared a more recent ancestor with the robust australopithecines than with *Homo* (see figure 3.08). The position of *A. africanus* remained uncertain either in a sister group with *Homo* or as a sister group of the other australopithecines.

Chamberlain and Wood (1987) performed a quantitative cladistic study with measurements from the cranium, mandible, and dentition and the most parsimonious cladogram was consistent with the phylogeny presented by Kimbel *et al.* (1984). Using Stringer's (1986) subdivision of early *Homo* the two species (*Homo habilis* and *Homo sp.*) were successive sister taxa to a clade including *H. erectus* and *H. sapiens* (see figure 3.09). Using their own subdivision of early *Homo* their *Homo sp.* appeared as the sister taxon of the robust australopithecines with *A. africanus* as a sister taxon. *H. habilis* appeared as a relatively primitive hominid sharing some derived characters with all taxa excluding *A. afarensis* (see figure 3.10).

Wood and Chamberlain (1987) reanalysed the data used in 1986 and found that the most parsimonious arrangement of taxa was one in which the robust australopithecines appeared as a sister group of *A. afarensis* (figure 3.08). When characters from over the entire cranium were used the results indicated that *A. afarensis* was not

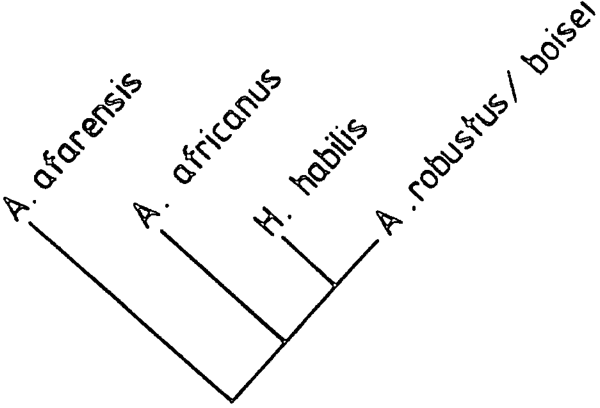


Figure 3.07 Cladogram of Skelton et al. (1986)

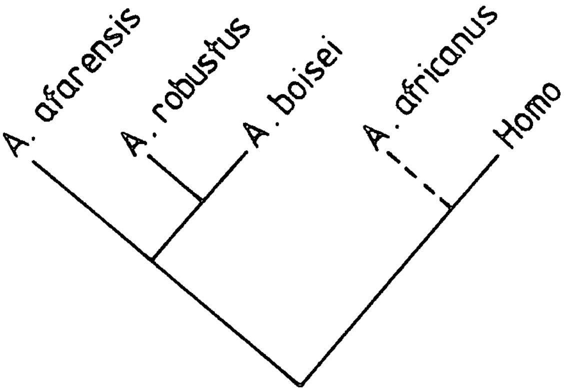


Figure 3.08 Cladogram of Wood and Chamberlain (1986)

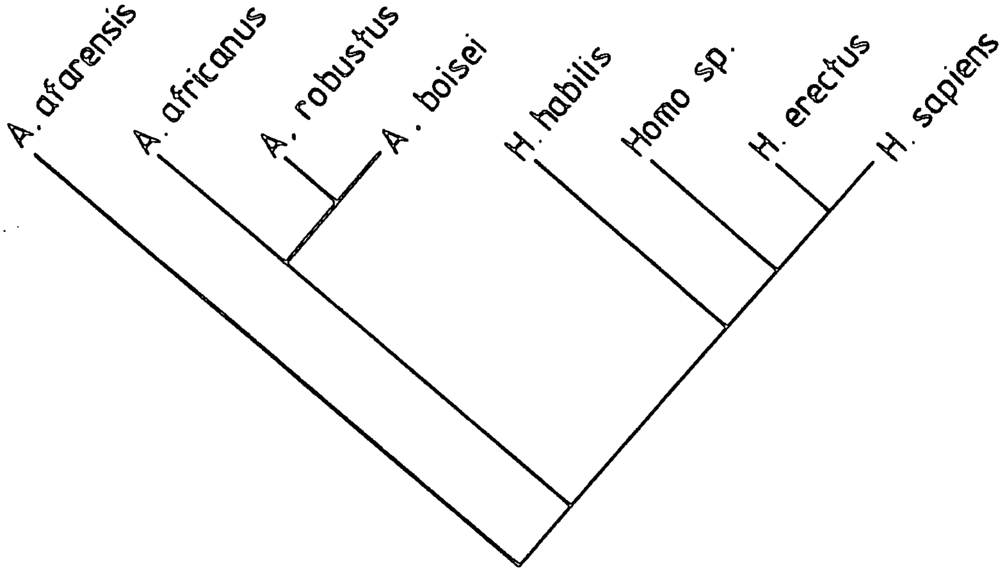


Figure 3.09 Cladogram using Stringer's subdivision of early Homo (From Chamberlain and Wood 1987)

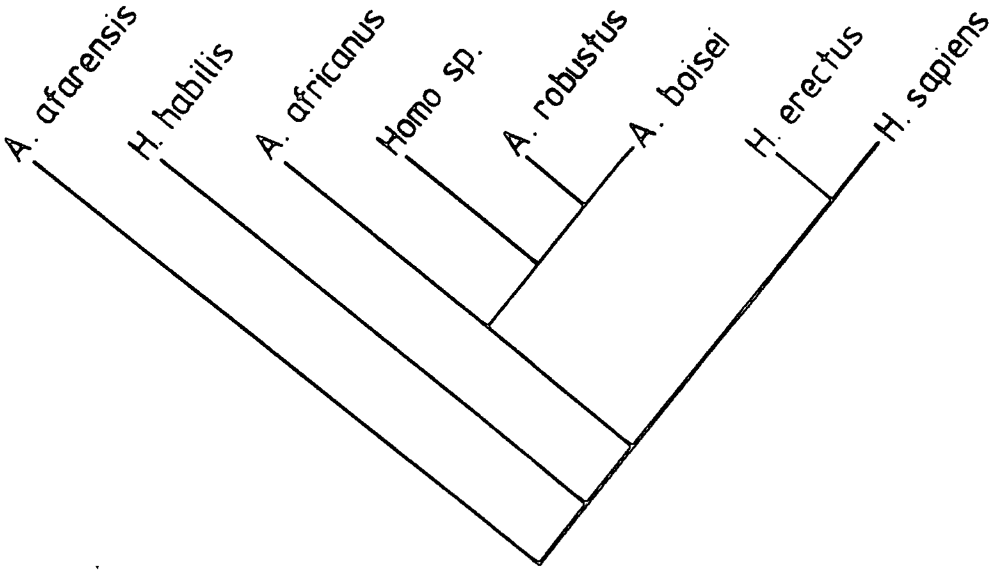


Figure 3.10 Cladogram using Chamberlain and Wood's (1987) subdivision of early Homo

wholly representative of the primitive hominid morphotype and possessed characters indicating a common ancestor shared with the robust australopithecines and that *A. africanus* may have shared a more recent common ancestor with *Homo* (see figure 3.11).

Stringer (1987) used nine different hominid groups allocated to the genus *Homo* in a numerical cladistic analysis using eleven, mostly cranial, characters. The three 'best' trees assign to one clade early archaic *H. sapiens* and early African *H. erectus* and Asian *H. erectus*. Another clade consists of Neanderthals, African late archaic *H. sapiens* Skhūl-Qafzeh, and modern *H. sapiens* (see figure 3.12).

Discussion

Since 1975, not only have new species been introduced and new fossil specimens, but also different methods have been adopted to perform cladistic analyses. The most recent methods include the use of computer programs which allow large quantities of data to be processed and the multitude of resultant cladograms to be assessed. Thus cladistic analysis has not remained static.

Many of the above analyses do not assess the potential problems caused by intraspecific variability. When a character has high intraspecific variability its usefulness in a cladistic analysis is questionable. Chamberlain (1987), however, applied Kazmierczak's transformation to mean measurements of cranial, mandibular, and dental characters before entering them into a cluster analysis, to assess problems of size variation and intraspecific allometry. This method resulted in female primates being consistently placed closest to their conspecific males. These transformed values were then converted into discrete character states and used in subsequent cladistic analyses (Chamberlain and Wood 1987, for example). Such an appraisal of intraspecific character variation prior to cladistic analysis is vital if inter-specific relationships are to be determined. If characters cannot correctly allocate sexual morphs of known groups with their conspecifics, their use in detailing fossil hominids relationships is doubtful.

3.3.7 Previous Cladistic Studies of the Hominoids

The idea that the great apes are more similar to each other than any is to *H. sapiens* was challenged in the 1960's on the basis of molecular evidence which indicated that African apes and humans were closer to each other than either was to the Orangutan (eg. Goodman 1963; Sarich and Wilson 1967).

Recent molecular studies tend to show the same thing, that is African apes and

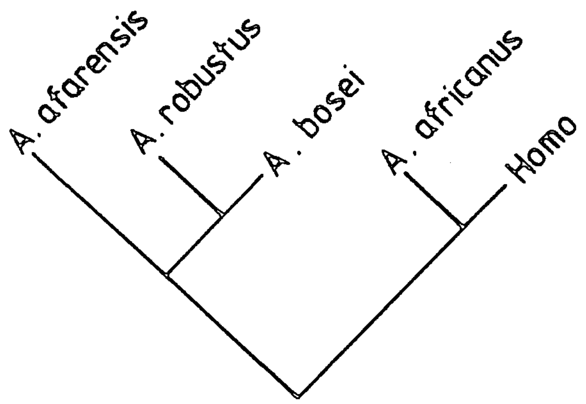


Figure 3.11 Cladogram from Wood and Chamberlain (1987)

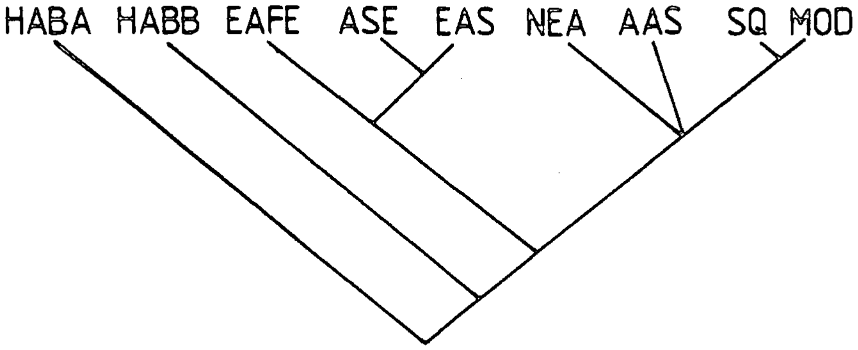


Figure 3.12 Cladogram from Stringer (1987)

HABA = H. habilis (Stringer 1986)
HABB = H. sp. (Stringer 1986)
EAFE = Early African H. erectus
ASE = Asian H. erectus
EAS = Early archaic H. sapiens
NEA = Neanderthals
AAS = African late archaic H. sapiens
SQ = Skhul-Qafzeh
MOD = Modern H. sapiens

man forming a monophyletic group, but the relationships within this clade are the subject of debate (see Andrews 1985, 1986, 1987; Martin 1986 for a review of the evidence).

A number of cladistic analyses have been performed over the past 20 years to determine the relationship between the great apes and humans using morphological and/ or molecular features. One view (eg. Sarich and Wilson 1967; Benveniste and Todaro 1976) showed the branching of African apes and man as a trichotomy (see figure 3.13). Another view (eg. Andrews 1986; Hasegawa et al. 1984) placed Chimpanzees closest to humans (see figure 3.14). A third hypothesis (eg. Schwartz *et al.* 1978; Martin 1986) showed *Gorilla* and *Pan* as a monophyletic group as a sister clade to humans (see figure 3.15). Kluge's (1983) analysis placed the great apes within a monophyletic group (see figure 3.16). Thus most studies showed a division of *Pongo* from the African ape and human clade within the great ape and human clade.

However, Schwartz (1984a, b, 1986) presented morphological and molecular evidence which suggested that *Pongo* was a sister taxon to *H. sapiens* (see figure 3.17) but analyses by Andrews (1986, 1987) and Groves (1986) did not support this view. Groves (1986) found some morphological evidence of a chimpanzee - human clade which was reinforced by electrophoresis data.

Andrews and Martin (1987) performed a cladistic analysis on extant and fossil hominoids. They combined morphological and molecular data and concluded from their analysis that the African apes formed a clade as the sister taxon of the human (including australopithecines, *Homo*, and *Paranthropus*) clade.

An analysis of fossil hominoids led to the conclusion that Proconsul was the sister taxon to the later Hominoidea. *Dryopithecus*, *Kenyapithecus*, *Heliopithecus* and *Afropithecus* shared derived characters with the great apes and humans and Andrews and Martin suggested that this was evidence of divergence of that clade from the gibbon lineage. *Sivapithecus* formed a sister group of the orangutan clade and it was suggested that the orang lineage diverged from the African ape and human lineage prior to 11.5 million years ago (see figure 3.18).

Thus whilst the majority of researchers accept a great ape and human clade and many an African ape and human clade, the relationships between *Pan*, *Gorilla*, and *H. sapiens* have not yet been resolved. The problem of the relationship between the African apes and humans continues to be controversial and may be the result of a short interval between *Gorilla* and Chimpanzee divergences (based on mitochondrial evidence) or else that Man, Chimps, and Gorillas diverged from the same species

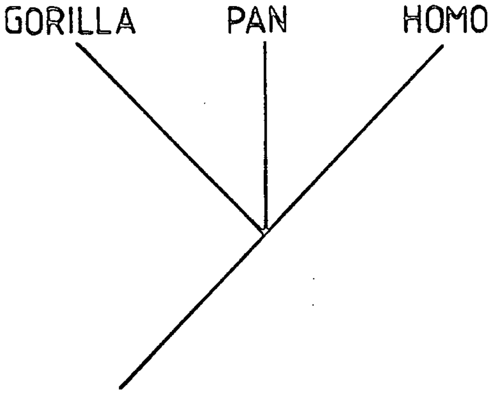


Figure 3.13 Relationship of African Apes and Humans Viewed as a Trichotomy

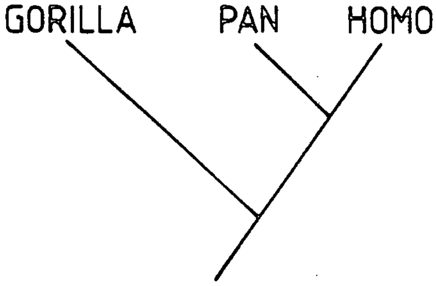


Figure 3.14 Cladogram from Andrews 1986

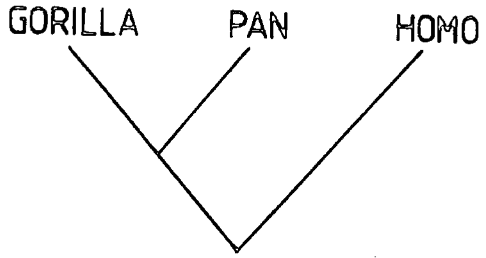


Figure 3. 15 Cladogram from Martin 1986

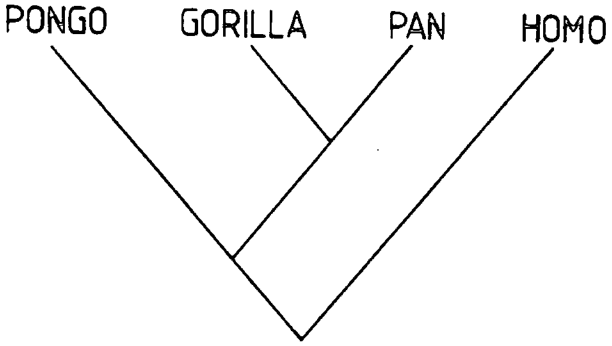


Figure 3. 16 Cladogram from Kluge 1983

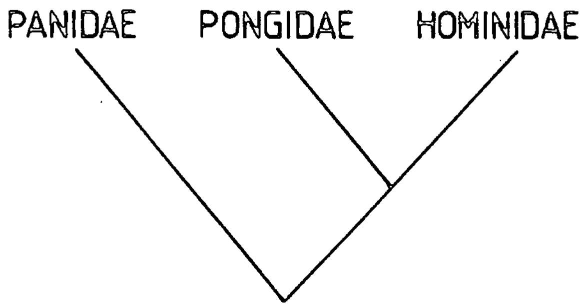


Figure 3.17 Cladogram from Schwartz 1986

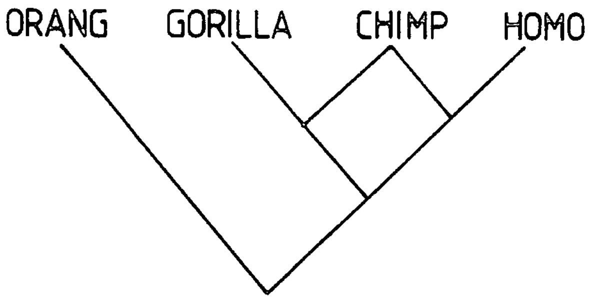


Figure 3.18 Cladogram from Andrews and Martin 1987

(based on the intergenic spacer region between ψ, η, and δ-globin genes) (Hasegawa *et al.* 1989).

Discussion

Each of these authors use a variety of traits in their cladistic analyses but until recently, little attention has been paid to intraspecific variation. Some authors, like Chamberlain (1987) and Andrews and Martin (1987) have either tested the ability of characters to group modern sexual morphs or have chosen to assign characters different weights, but little discussion has been made of the effect the use of variable characters will have on the results of cladistic analyses (see Trinkaus 1990).

Thus not only should an assessment be made of the amount of variation each character shows within a population, that is the identification of variable and non-variable traits, but also an assessment should be made of the effect on the cladogram of using such traits, either separately, or in combination. This preliminary analysis should lead to at least a better understanding of why some groups share certain synapomorphies if not providing a more realistic assessment of fossil hominid relationships. Thus, in Chapter 7, I attempt to assess the effects of using variable, non-variable, and both types of traits in cladistic analyses.

3.4 Conclusions

Thus inter- and intra-specific variability in fossil hominids and modern hominoids will be investigated using univariate and multivariate analytical techniques in order to address the first two aims of this thesis. The third aim of this thesis will be addressed in a cladistic analysis and the methods used in that analysis will be described in further detail in the next chapter.

CHAPTER 4: MATERIALS AND METHODS

4.1 Introduction

The present study involves an analysis of inter- and intra-specific diversity among the early fossil hominids based upon models derived from samples of modern *H. sapiens* and pongids. Metrical cranial characters are used in order to assess the functional and systematic/ phyletic implications of their variability within the available early hominid sample (*A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, *H. habilis*, and *H. erectus*) using univariate, multivariate, and cladistic analytical techniques. This chapter lists the fossil and modern skeletal material used, outlines the characters measured and their definitions, and explains the statistical and cladistic analyses used to assess patterns of morphological variation in this thesis.

4.2 Materials

4.2.1 Fossil Hominids

The fossil hominid specimens were examined at the Kenya National Museum in Nairobi, Kenya, the University of the Witwatersrand in Johannesburg and the Transvaal Museum in Pretoria, South Africa. Casts of some of the Olduvai material as well as a selection of the Hadar material were examined at the Kenya National Museum. A cast of Sangiran 17 was examined at the British Museum (Natural History) in London and other cast material was examined at Durham University.

The species of fossils in this study include all of the available East and South African australopithecine material (with the exception of specimens from Omo). Specimens from the genus *Homo* include *H. erectus* (African), some Asian *H. erectus* specimens, the Mauer mandible, and specimens assigned to *H. habilis* (including specimens of 'early Homo'). The australopithecine fossils include those assigned to the taxa *A. afarensis*, *A. africanus*, *A. robustus*, and *A. boisei.* No fossils from the taxa of *Homo sapiens neanderthalensis* are examined.

Fossils from the sites of Laetoli, Tanzania and Hadar, Ethiopia are entered in Table 4.01 as *A. afarensis* (Johanson *et al.* 1979). Most of the specimens from Sterkfontein, South Africa are entered in the table as *A. africanus* (Day 1986) except for STW 53 which Chamberlain (1987) calls 'early *Homo*' but which I call *H. habilis* following Hughes and Tobias (1977). The Makapansgat specimens are all entered in the table as *A. africanus* while those from Kromdraai are entered as *A. robustus* (Day 1986). Most of the Swartkrans specimens are entered as *A. robustus* (Day 1986)

TABLE 4.01: Number of Measurements per Fossil Specimen per Region

Specimen number	Taxon	Location	Mandible	Palate	Base	Vault	Face	Total
ER 403	A. b.	KNM	4					4
ER 404	A. b.	KNM	4					4
ER 405	A. b.	KNM		9			2	11
ER 406	A. b.	KNM		7	24	24	26	81
ER 407	A. b.	KNM			20	14		34
ER 725	A. b.	KNM	4					4
ER 726	A. b.	KNM	4					4
ER 727	A. b.	KNM	1					1
ER 728	A. b.	KNM	3					3
ER 729	A. b.	KNM	12					12
ER 730	H. er.	KNM			1	6		7
ER 731	H. er.	KNM	2					2
ER 732	A. b.	KNM			14	14	19	46
ER 733	A. b.	KNM	2					2
ER 801	A. b.	KNM	4					4
ER 805	A. b.	KNM	3					3
ER 807	H. er.	KNM		1				1
ER 810	A. b.	KNM	4					4
ER 817	H. er.	KNM	2					2
ER 818	A. b.	KNM	5					5
ER 819	A. b.	KNM	1					1
ER 992	H. er.	KNM	9					9
ER 1468	A. b.	KNM	3					3
ER 1469	A. b.	KNM	4					4
ER 1470	H. h.	KNM		2	8	17	18	45

TABLE 4.01 Cont'd: Number of Measurements per Fossil Specimen per Region

Specimen number	Taxon	Location	Mandible	Palate	Base	Vault	Face	Total
ER 1478	A. b.	KNM		1				1
ER 1501	H. er.	KNM	5					5
ER 1502	H. er.	KNM	2					2
ER 1506	H. er.	KNM	2					2
ER 1507	H. er.	KNM	2					2
ER 1590	H. h.	KNM				2		2
ER 1801	H. h.	KNM	4					4
ER 1802	H. h.	KNM	8					8
ER 1803	H. h.	KNM	1					1
ER 1805	H. h.	KNM	10	7	17	15	10	59
ER 1806	A. b.	KNM	3					3
ER 1813	H. h.	KNM		9	24	24	23	80
ER 2602	A. b.	KNM				2		2
ER 3230	A. b.	KNM	9					9
ER 3729	A. b.	KNM	4					4
ER 3732	H. h.	KNM				8	7	15
ER 3733	H. er.	KNM		6	24	23	27	80
ER 3883	H. er.	KNM			22	24	17	63
ER 3889	A. b.	KNM	2					2
ER 3891	A. b.	KNM		3	2			5
ER 3892	H. er.	KNM				1		1
ER 3950	H. er.	KNM	1					1
OH 5	A. b.	KNM*		9	24	24	27	84
OH 9	H. er.	KNM*			19	21	6	46
OH 12	H. er.	KNM		1	2	4		7

TABLE 4.01 Cont'd: Number of Measurements per Fossil Specimen per Region

Specimen number	Taxon	Location	Mandible	Palate	Base	Vault	Face	Total
OH 16	H. h.	KNM			3	9	1	13
OH 22	H. er.	KNM	10					10
OH 23	H. er.	KNM	1					1
OH 24	H. h.	KNM		9	22	16	23	70
OH 51	H. er.	KNM	1					1
BK 67	H. er.	KNM	11					11
BL 8518	H. er.	KNM	10					10
Peninj	A. b.	KNM	11					11
LH 4	A. afar.	KNM	9					9
LH 13	A. afar.	KNM	1					1
LH 29	H. er.	KNM	2					2
AL 128.23	A. afar.	KNM*	5					5
AL 145.35	A. afar.	KNM*	5					5
AL 166.9	A. afar.	KNM*			2			2
AL 188.1	A. afar.	KNM*	4					4
AL 198.1	A. afar.	KNM*	9					9
AL 199.1	A. afar.	KNM*		8				8
AL 200.1	A. afar.	KNM*		9			2	11
AL 207.13	A. afar.	KNM*	9					9
AL 266.1	A. afar.	KNM*	8					8
AL 277.1	A. afar.	KNM*	5					5
AL 288.1	A. afar.	KNM*	12					12
AL 311.1	A. afar.	KNM*	3					3
AL 333-2	A. afar.	KNM*		2				2
AL 333-45	A. afar.	KNM*			17	10		27

TABLE 4.01 Cont'd: Number of Measurements per Fossil Specimen per Region

Specimen number	Taxon	Location	Mandible	Palate	Base	Vault	Face	Total
AL 333-84	A. afar.	KNM*				2		2
AL 333-86	A. afar.	KNM*		4				4
AL 333w1	A. afar.	KNM*	3					3
AL 333w12	A. afar.	KNM*	5					5
AL 333w58	A. afar.	KNM*	1					1
AL 333w60	A. afar.	KNM*	9					9
AL 400.1	A. afar.	KNM*	8					8
Reconstr.	A. afar.	DUR*	12	9	20	18	20	79
STS 5	A. af.	TM		7	24	24	27	82
STS 7	A. af.	TM	6					6
STS 17	A. af.	TM		3			13	16
STS 19	A. af.	TM			20			20
STS 25	A. af.	TM			12	4		16
STS 26	A. af.	TM			2	2		4
STS 36	A. af.	TM	12					12
STS 52	A. af.	TM	11	8			13	32
STS 53	A. af.	TM		9			2	11
STS 63	A. af.	TM					3	3
STS 71	A. af.	TM		3	4	22	23	52
MLD 1	A. af.	UW			1	6		7
MLD 3	A. af.	UW				2		2
MLD 6	A. af.	UW		5			6	11
MLD 9	A. af.	UW		5			2	7
MLD 18	A. af.	UW	8					8
MLD 19	A. af.	UW	2					2
MLD 22	A. af.	UW	1					1

TABLE 4.01 Cont'd: Number of Measurements per Fossil Specimen per Region

Specimen number	Taxon	Location	Mandible	Palate	Base	Vault	Face	Total
MLD 29	A. af.	UW	2					2
MLD 34	A. af.	UW	2					2
MLD 37/8	A. af.	UW			24	14		38
MLD 40	A. af.	UW	10					10
STW 13	A. af.	UW		4			7	11
STW 14	A. af.	UW	3					3
STW 53	H. h.	UW		7	2	2	5	16
STW 73	A. af.	UW		7				7
STW 109	A. af.	UW	1					1
STW 252	A. af.	UW		2		3	2	7
STW 384	A. af.	UW	1					1
STW 391	A. af.	UW		1			1	2
STW 404	A. af.	UW	4					4
SK 11	A. r.	TM		4			1	5
SK 12	A. r.	TM	12	2			6	20
SK 15	H. er.	TM	7					7
SK 23	A. r.	TM	8					8
SK 34	A. r.	TM	7					7
SK 45	H. er	TM	2					2
SK 46	A. r.	TM		8	2	3	7	20
SK 48	A. r.	TM		9	5	10	27	51
SK 65	A. r.	TM		2				2
SK 79	A. r.	TM		9			2	11
SK 83	A. r.	TM		9	4	2	9	24
SK 844	A. r.	TM	2					2
SK 847	H. h.	TM		4	14	6	23	47
SK 858	A. r.	TM	1					1
SK 876	A. r.	TM	2					2

TABLE 4.01 Cont'd: Number of Measurements per Fossil Specimen per Region

Specimen number	Taxon	Location	Mandible	Palate	Base	Vault	Face	Total
SKW 12	A. r.	TM					1	1
TM 1511	A. a.	TM		4	2		12	18
TM 1517	A. r.	TM	3	5	18	4	10	40
TM 3009	A. a.	TM		1				1
SAN 17	H. er.	BMNH*		8	20	20	20	68
SkullI(L)	H. er.	DUR*			6	17		23
SkullII(L)	H. er.	DUR*			6	18		24
SkullIII(L)	H. er.	DUR*			5	16		21
Skull3(E)	H. er.	DUR*			6	19		25
Pith I	H. er.	DUR*				10		10
Pith II	H. er.	DUR*			6	14		20
Mauer	H. er.	DUR*	12					12
HI	H. er.	DUR*	12					12
GI	H. er.	DUR*	11					11

* Indicates a cast

DUR = Durham University

KNM = Kenya National Museum

TM = Transvaal Museum

UW = University of the Witwatersrand

BMNH = British Museum of Natural History except for SK 15 and SK 45 which are entered as *H. erectus* (Robinson 1961) and SK 847 which I call *H. habilis* (Howell 1978a). All the specimens from Olduvai, Tanzania are assigned to *A. boisei*, *H. habilis*, or *H. erectus* as in Day (1986) except OH 16 which Day lists as *Homo* but which I call *H. habilis* following Leakey *et al.* (1964) and Stringer (1987). The Baringo specimens are entered into Table 4.01 as *H. erectus* (Day 1986) and the Peninj mandible as *A. boisei* (Day 1977).

Most of the specimens from Koobi Fora, Kenya have been assigned in the literature to genera but not to species (eg. Day 1986). For the purpose of this present analysis, most of the specimens referred to by Day (1986) as *Australopithecus* are entered into table 4.01 as *A. boisei* and those referred to as *Homo*, as *H. erectus.* The exceptions are KNM-ER 1470, 1590, 1801, 1802, 1803, 1805, 1813, and 3732. Most of these specimens have been called either *H. habilis* or 'early *Homo*' by various workers (eg. Stringer 1987, Chamberlain 1987). KNM-ER 1801 has been said to resemble KNM-ER 1802 (Leakey 1974) so I have listed this specimen as *H. habilis.* KNM-ER 1803 is listed by Day (1986) as *incertae sedis* but since it was found with KNM-ER 1801 and 1802, and because only one measurement was obtained from it, I have listed it as *H. habilis.* Finally, the Mauer mandible and the Chinese and Javanese specimens are listed as *H. erectus*, as in Day (1986).

Measurements were taken on adult, juvenile, and infant specimens where age was judged by dental development or cranial suture closure where applicable but only adult specimens were included in this study. For example, OH 5 was included because there was evidence of wear on the left third molar but OH 13 was excluded since there was no indication that the teeth had erupted into wear. A number of specimens had a taxonomic status of *Australopithecus sp.*, *Hominidae*, or *insertae sedis* but they were not included in this analysis. Specimens with only a few available measurements were included in order to assess within species variation for each variable and table 4.01 lists the number of measurements per specimen per region.

Table 4.02 lists the number of specimens of each hominid taxon per region. The taxa are unevenly represented in each region, with all taxa having at least four representatives per region, except *A. afarensis* which has only two specimens with any facial measurements and only three specimens with base and vault measurements; one of these in each of the regions being the reconstructed cranium. Measurements taken on the reconstructed male *A. afarensis* cranium (Kimbel et al. 1984) are used in order that at least one *A. afarensis* specimen is included in all analyses. Not all measurements are utilised, however, as I only feel justified in including measurements when one or more of the landmarks lies on the fossil material but not when the

TABLE 4.02: Number of Specimens of Fossil Taxon per Region

Taxon	Mandible	Palate	Base	Vault	Face
A. afarensis	15	5	3	3	2
A. africanus	13	13	8	8	12
A. robustus	7	8	4	4	8
A. boisei	20	5	5	5	4
H. habilis	4	6	7	8	8
H. erectus	19	4	11	13	4

landmarks lie only on the reconstructed matrix.

4.2.2 Primates and Humans

Ten male and ten female individuals from the species of *Gorilla gorilla*, *Pongo pygmaeus*, and *Pan troglodytes* were examined at the British Museum (Natural History) in London. Individuals were chosen for their completeness, although it was necessary to include some specimens with damage to only one region of measurement. Among the primate sample, species were not from the same locality, nor were they collected at the same time so they do not represent one breeding population. With regard to sagittal cresting among the male primates, a variety of males of different sizes were selected to assess variation in this area as well as the effect on other areas of the skull.

The *H. sapiens* population originated from the Poundbury site and were examined at the British Museum (Natural History) in London.

The age of all specimens was determined by dental development and sex was determined from the museum records. A list of the individual crania and their catalogue numbers can be found in Appendix 1.

4.3 Measurements

4.3.1 Selection of Measurements

Measurements were selected in order to analyse the skull in functional terms but also to take into account the fragmentary nature of the hominid fossil record. For this reason I defined areas which could then be analysed in terms of their functional morphology. Originally these consisted of four regions of the skull: masticatory system, base, vault, face, but, because of the fragmentary nature of the fossil material, the masticatory system was further subdivided into the sections of mandible and palate. This meant that characters could be examined individually in univariate analyses and also in combination, either region by region or combined, to examine the total morphological pattern of variation in the skull.

I decided to use metric traits because they were easily quantifiable and more objective than non-metric traits. I attempted to quantify some non-metric traits, for example the height of the articular eminence, since these types of characters were known to be variable in hominoids and also are used as taxonomic indicators by some workers.

An attempt is made to have each region equally represented in number of measurements. Thus the cranium is divided into five sections over the four regions mentioned above, with approximately the same number of measurements per region: masticatory system (21) [mandible (12), palate (9)], base (24), vault (24), and face (27). Measurements are selected from lists available from Tobias (1967), Howells (1968), Dean and Wood (1981, 1982), Brothwell (1981), Skelton *et al.* (1984), are depicted in figures 4.01 - 4.05, and listed in table 4.03.

4.3.2 Measurement Definitions

Landmarks are defined in each region and chosen not only because they are easy to locate and because they are thought to be homologous between fossil hominids and extant primates, but because they are thought to have functional/ systematic significance. Most of the landmarks and definitions of measurements are based on standard definitions found in the literature. Some measurements, for example, bizygomatic breadth at the plane of the orbits (F6) obtained from Rak (1983), does not have landmark labels so these are assigned by me. As seen in Appendix 2, measurements are listed by number (eg. F1 to F27), then descriptive definition, and then by their landmarks. Definitions of each landmark are also found in Appendix 2. In the following analyses, measurements are referred to by their number or descriptive definition, or both where deemed necessary.

All measurements were taken using sliding, spreading, or coordinate calipers, or cloth tape measures. Caliper measurements were recorded to the nearest 1 mm. The cloth tape measure was used to measure the arc from FMT to PO (V15) along the temporal muscle mark (or crest) and the results were not as precise as the other arc measurements. I estimate that this measurement could vary by ± 2.5mm. Bilateral measurements on incomplete fossils were often made by doubling from the midline but if the fossil was only slightly damaged an estimated measurement was taken. These measurements are indicated by square brackets in Appendix 3. Measurements were recorded on data sheets prior to their being entered and stored on the Durham University mainframe computer. Measurements were rechecked on data sheets as well as on printouts of the computer files in order to minimise errors.

4.4 Methods

4.4.1 Statistical Analyses

The analyses in the following chapters aim to assess within- and between-species variation of the fossil hominids using models derived from extant hominoid samples. The study is divided into two chapters of univariate and multivariate statistical analyses. The first type of analysis, in Chapter 5, allows the assessment of individ-

Figure 4.01 : Mandibular Measurements

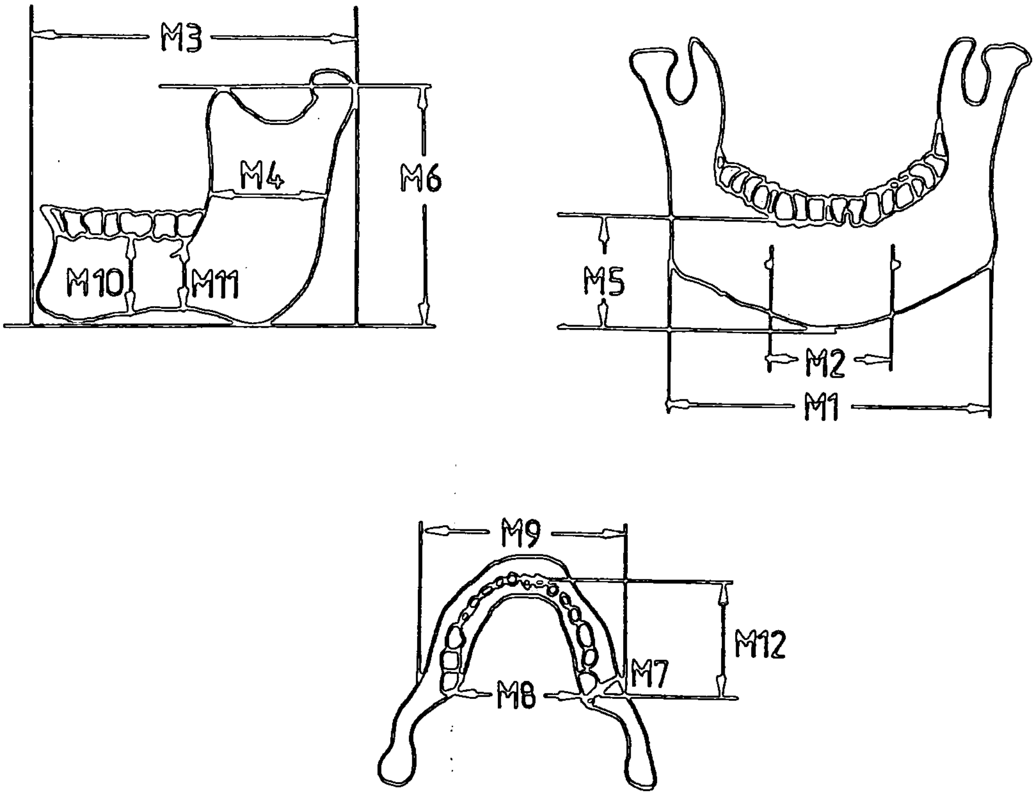


Figure 4.02: Palatal Measurements

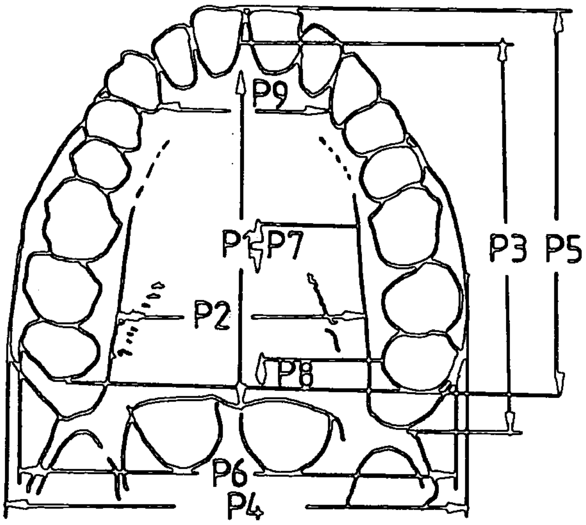
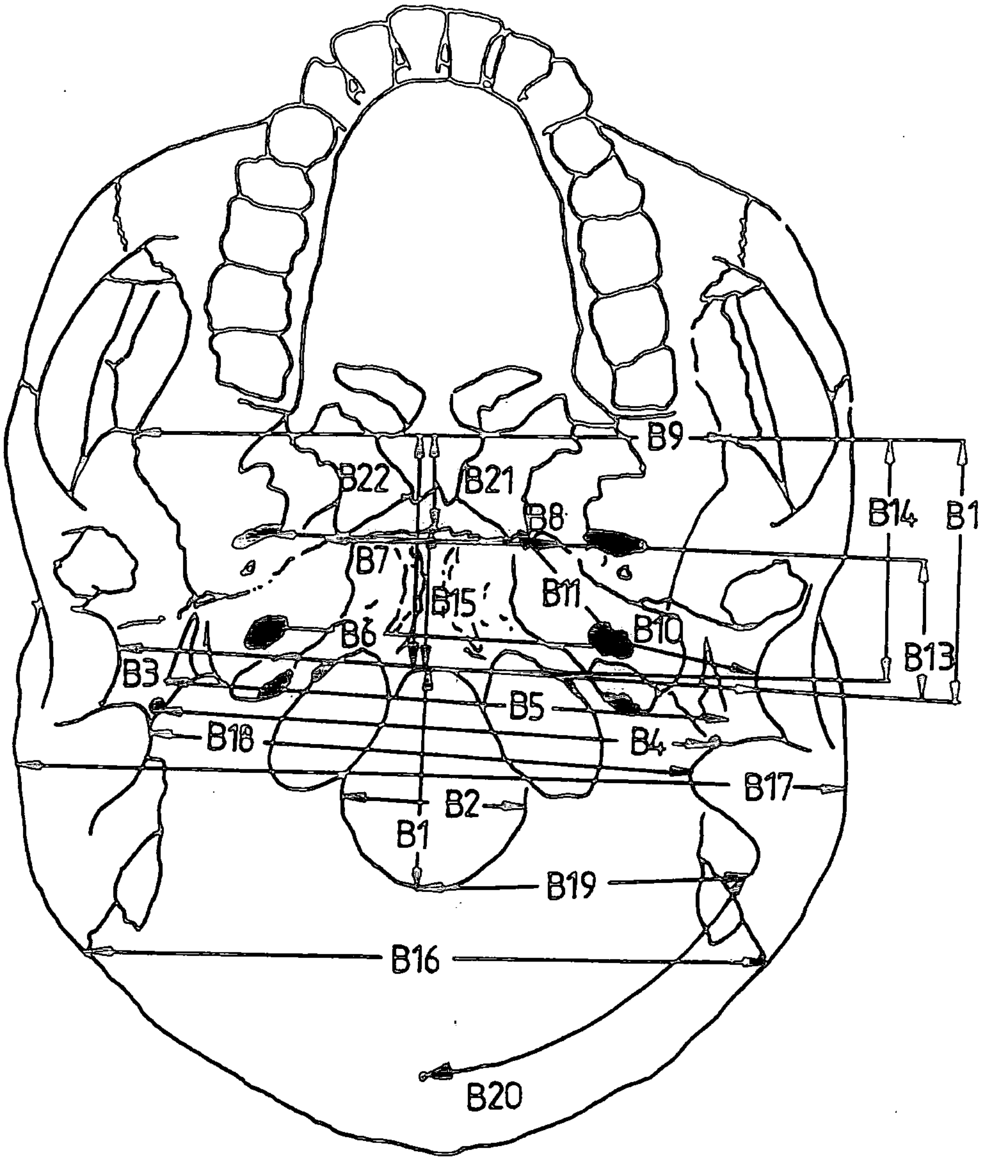


Figure 4.03: Base Measurements



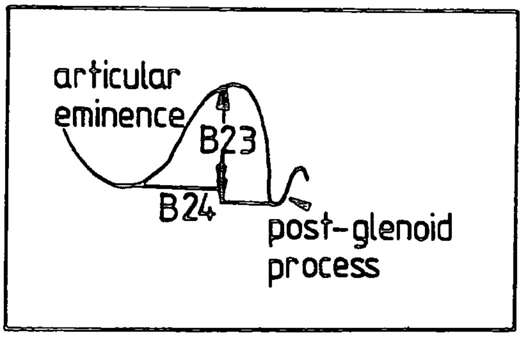


Figure 4.04: Vault Measurements

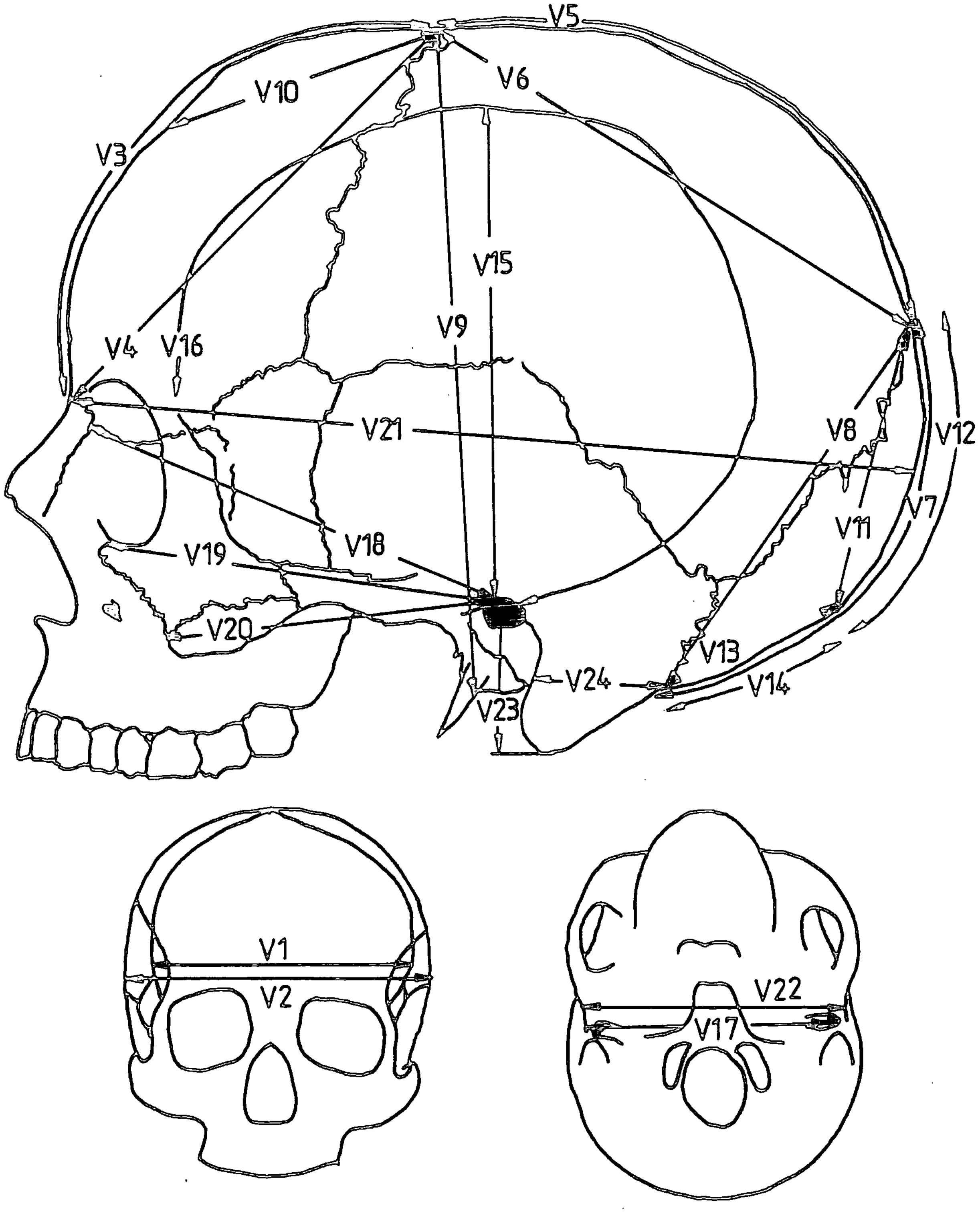


Figure 4.05a: Face Measurements

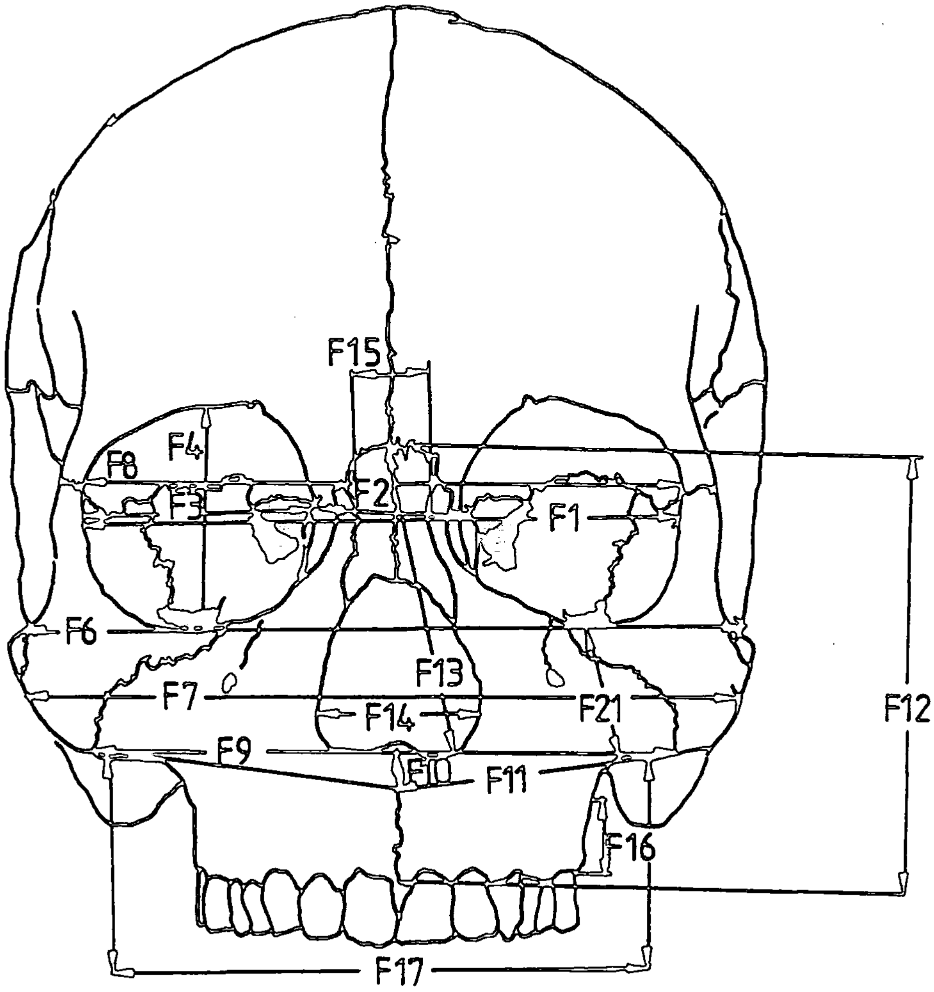


Figure 4.05b: Face Measurements

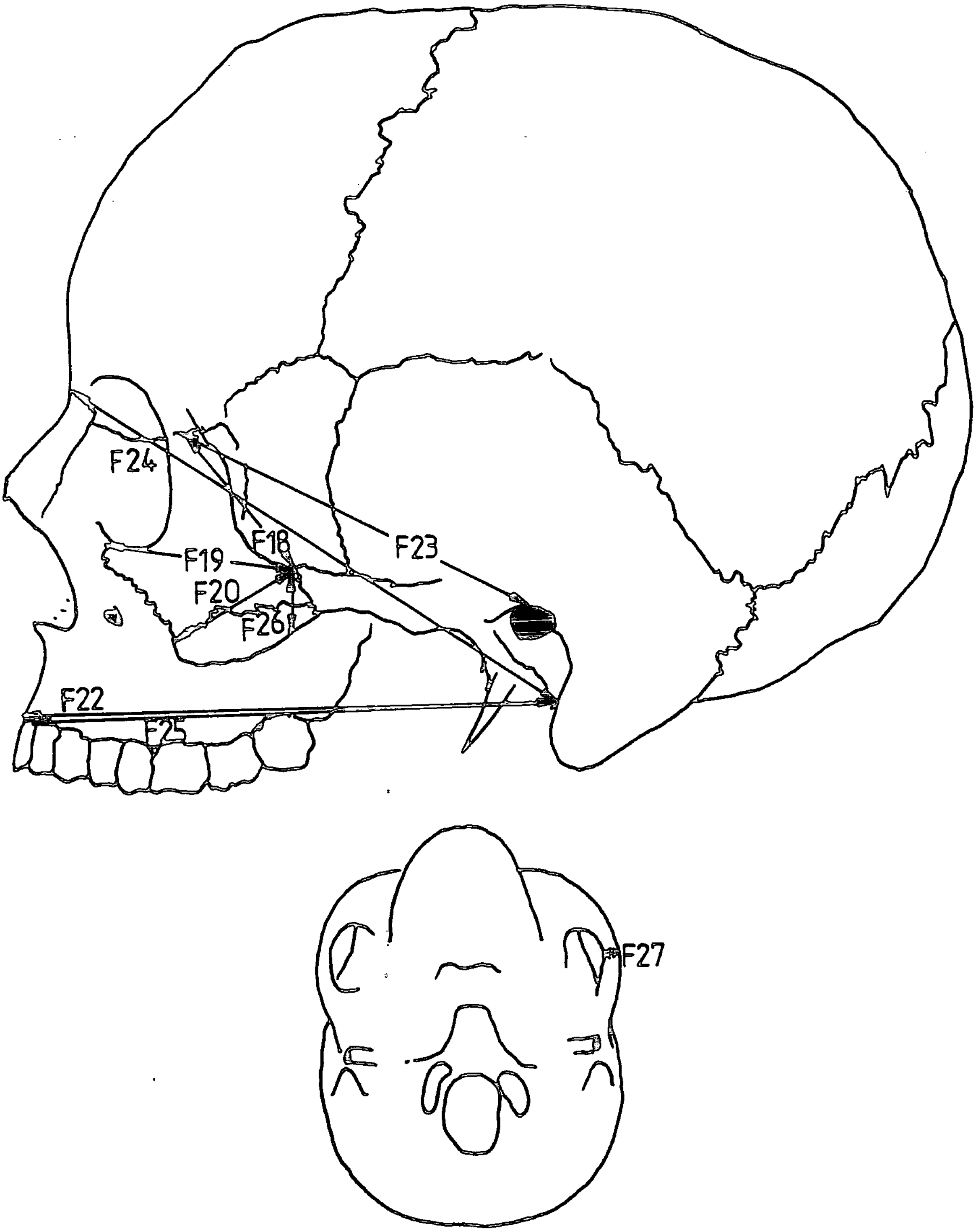


TABLE 4.03: List of Measurements

M1	Bigonial breadth. (= Brothwell 1981: XVIII')
M2	Foramen mentalia breadth. (= Brothwell 1981: XIX')
M3	Maximum length of the mandible. (= Brothwell 1981: XXII')
M4	Minimum ramus breadth. (= Brothwell 1981: XX')
M5	Symphyseal height. (= Brothwell 1981: XXI')
M6	Coronoid height. (= Brothwell 1981: XXIII')
M7	Maximum thickness of the mandibular corpus. (Adapted from Leakey and Leakey 1978).
M8	Maximum internal breadth from alveolar margins of the mandible. (to provide measurement similar to P2)
M9	Maximum external breadth from alveolar margins of the mandible. (to provide measurement similar to P4)
M10	Depth of corpus at M1. (= Chamberlain 1987: M2)
M11	Depth of corpus at M3. (= Chamberlain 1987: M3)
M12	Arcadal length. (Adapted from Tobias 1967: arcadal length (Laing))
P1	Palate length. (= Brothwell 1981: XIII)
P2	Maximum lingual breadth between alveolar margins. (Adapted from Tobias 1967: palatal breadth)
P3	Maxillo-alveolar length. (Tobias 1967)
P4	Maximum external breadth between outer margins. (Howells 1968)
P5	Arcadal length. (= Tobias 1967: arcadal length (Laing)
P6	Maximum arcadal breadth. (Adapted from Tobias 1967: arcadal breadth (Laing).
P7	Palatal depth at M1. (metric version of non-metric trait of Skelton *et al.* 1986)
P8	Palatal depth at M3. (metric version of non-metric trait of Skelton *et al.* 1986)
P9	Bicanine breadth. (= Chamberlain 1987: P3)
B1	Foramen magnum length. (=Dean and Wood 1981: 1.)
B2	Foramen magnum width. (=Dean and Wood 1981: 2.)
B3	Bitympanic width. (=Dean and Wood 1981: 3.)
B4	Bistylomastoid width. (=Dean and Wood 1981: 4.)
B5	Bistyloid width. (=Dean and Wood 1981: 5.)
B6	Bicarotid canal width. (=Dean and Wood 1981: 6.)
B7	Bipetrous width from apex to apex of the petrous temporal bones. (=Dean and Wood 1981: 7.)
B8	Biforamen ovale width (centre). (=Dean and Wood 1981: 8.)
B9	Biinfratemporal fossa width. (=Dean and Wood 1981: 9.)
B10	Length of the tympanic plate from the lateral end of the tympanic to the centre of the carotid canal. (=Dean and Wood 1981: 10.)

TABLE 4.03 Cont'd: List of Measurements

B11	Length along the petrous temporal bone from the centre of the carotid canal to apex. (=Dean and Wood 1981: 11.)
B12	Distance between biinfratemporal line and bitympanic line. (=Dean and Wood 1981: 12.)
B13	Distance between biforamen ovale line and bitympanic line. (=Dean and Wood 1981: 13.)
B14	Distance between biinfratemporal line and basion. (=Dean and Wood 1981: 14.)
B15	Basioccipital length. (=Dean and Wood 1981: 15.)
B16	Biasterionic breadth. (= Brothwell 1981: XIII')
B17	Maximum breadth across supramastoid crests. (Tobias 1967)
B18	Bimastoid breadth. (Tobias 1967)
B19	Nuchal crest width. (Adapted from Bilsborough 1971)
B20	Lateral nuchal crest arc. (Adapted from Bilsborough 1971)
B21	Sphenooccipital synchrondosis-staphlyon chord. (see B22)
B22	Staphlyon-basion chord. (B15, B21, and B22 - metric measure of basicranial flexion from Skelton *et al.* 1986)
B23	Articular eminence height. (Adapted from Ashton and Zuckerman 1954)
B24	Post-glenoid process height. (Adapted from Ashton and Zuckerman 1954)
V1	Maximum frontal breadth. (Howells 1968)
V2	Maximum biparietal breadth. (= Brothwell 1981: II)
V3	Frontal arc. (= Brothwell 1981: II')
V4	Frontal chord. (= Brothwell 1981: V')
V5	Parietal arc. (= Brothwell 1981: III')
V6	Parietal chord. (= Brothwell 1981: VI')
V7	Occipital arc. (= Brothwell 1981: IV')
V8	Occipital chord. (= Brothwell 1981: VII')
V9	Basi-bregmatic height. (= Brothwell 1981: III)
V10	Supraglabellar-bregmatic chord. (Bilsborough 1971)
V11	Inion chord. (Tobias 1967)
V12	Inion arc. (Tobias 1967)
V13	Nuchal chord. (Tobias 1967)
V14	Nuchal arc. (Tobias 1967)
V15	Height of temporal muscle mark. (Bilsborough 1971)
V16	Temporal muscle mark arc. (Bilsborough 1971)
V17	Biporionic breadth. (= Brothwell 1981: XV')
V18	Porion-dacryon chord. (Adapted from Howells 1968: dacryon radius)
V19	Porion-zygoorbitale chord. (Adapted from Howells 1968: zygoorbitale radius)

TABLE 4.03 Cont'd: List of Measurements

V20	Porion-zygomaxillare chord. (Adapted from Howells 1968: zygomaxillare radius)
V21	Naso-occipital length. (Howells 1968)
V22	Biauricular breadth. (Howells 1968)
V23	Mastoid length. (Howells 1968)
V24	Mastoid width. (Howells 1968)
F1	Maximum horizontal breadth of the orbits. (Adapted from Tobias 1967: inner orbital breadth)
F2	Interorbital breadth. (= Brothwell 1981: XII')
F3	Maximum orbital breadth. (= Brothwell 1981: XI)
F4	Maximum orbital height. (Howells 1968)
F5	Glabella projection. (Howells 1968)
F6	Bizygomatic breadth at the plane of the orbits. (Rak 1983)
F7	Maximum bizygomatic breadth. (= Brothwell 1981: VIII)
F8	Upper facial breadth. (= Chamberlain 1987: F1)
F9	Bimaxillary chord. (= Brothwell 1981: VII)
F10	Zygomaxillary subtense. (Howells 1968)
F11	Subspinale-zygomaxillare chord. (Howells 1968: to complete zygomaxillary angle)
F12	Upper facial height. (= Brothwell 1981: VI)
F13	Nasal Height. (= Brothwell 1981: XV')
F14	Maximum nasal breadth. (= Brothwell 1981: X)
F15	Simotic chord. (= Brothwell 1981: X')
F16	Distance from the root of the zygomatic to the alveolar margin.
F17	Bizygomatic tubercle breadth. (Adapted from Rak 1983)
F18	Superior malar length. (Howells 1968)
F19	Maximum malar length. (Howells 1968)
F20	Inferior malar length. (Howells 1968)
F21	Minimum cheek height. (Howells 1968)
F22	Superior facial length. (Howells 1968)
F23	Lateral facial length. (Tobias 1967)
F24	Basi-nasal length. (= Brothwell 1981: IV)
F25	Basi-alveolar length. (= Brothwell 1981: V)
F26	Zygomatic arch depth. (Adapted from Bilsborough 1971)
F27	Zygomatic arch thickness. (Adapted from Bilsborough 1971)

ual variables and thus allows the inclusion of some of the most fragmentary fossil specimens. This chapter is further subdivided into two sections, the first assessing within-species variation in the extant hominoids and fossil groups, the second an analysis of between-species variation.

The second analysis, Chapter 6, precludes the inclusion of all but the most complete fossil specimens. The first section of this chapter involves a principal components analysis which minimises between-species differences and maximises within-species differences and so allows the homogeneity of the fossil groups to be assessed.

The Principal Components Analysis (PCA) technique allows individual specimens to be entered into an analysis which, like cluster analysis, groups together individuals who are most similar to one another. Unlike cluster analysis, it allows an attempt to discuss why specimens group together; that is, to determine if there is a biological basis behind the clusters. PCA forms linear combinations of the observed variables where the first Principal Component (PC) is the combination that accounts for the largest amount of variance in the sample. PC2 accounts for the next largest amount of variation and is uncorrelated with the first PC. Successive components explain smaller and smaller amounts of the total sample variance.

The PCA in the present study was carried out using the SPSSX FACTOR program. This program allows the construction of correlation and PC matrices and the calculation of eigenvalues. It also calculates the PC scores of each specimen for each PC which can then be plotted.

The correlation matrix identifies which variables are most closely correlated with one another. The calculation of eigenvalues determines how much variance each PC accounts for. Not all PC's need to be examined since many will only account for only a very small percentage of the total variance. There are a variety of ways to choose the number of PC's which best describe the data. I have chosen to select the number of PC's which account for approximately ninety percent of the total sample variance. Other methods include choosing PC's with eigenvalues of 1 or greater but this may mean only one or two PC's will be chosen.

The PC matrix shows the relationship between the variables and the PC's but it is usually difficult to identify the PC's based on this matrix; often characters do not appear to be correlated in any interpretable pattern. The PC matrix is therefore rotated to make the identification of PC's, or underlying biological constructs, easier. During rotation the percentage of total variance accounted for by each PC does not change. What does change is the percentage of variance accounted for by each character, that is, the character's loading on each PC. The rotation redistributes the explained variance for the individual characters in order to minimise the number of variables that have high loadings on each PC so that few, if any, variables will have large loadings on more than one PC. Once the rotation has been completed, characters with the highest loadings on a PC will explain most of the variance on that PC and these characters can be discussed in biological terms (Norusis 1988). The rotation process is usually associated with Factor analysis but according to Reyment *et al.* (1984) it is also appropriate and useful in a Principal Components Analysis.

PCA picks axes out of 'n' dimensional space which maximise the variance of all the individuals entered into the analysis. If all the modern comparators are entered into the analysis, then they will have the most influence on the PC extraction since the number of fossils is small. The number of fossils that can be entered into the analysis is restricted because the program rejects individuals which have missing values. When all the modern groups are entered into the analysis then the main thing being examined and described are the differences between them, and not the fossil hominids. In order to place more emphasis on the fossil variance I made two decisions: 1. to maximise the number of fossils entered into the analysis; and 2. to select only one of the modern groups for comparison.

The first decision was implemented by: 1) dividing the skull into regions; and 2) by selecting measurements that, while describing overall dimensions of a region, allowed the most fossils to be included, so maximising the number of fossils which could be examined with the minimum of information loss.

With respect to the second decision I chose to include only male and female *Gorilla*, the most sexually dimorphic of all the modern comparators. By including *Gorilla* in the analysis of within-group variability and using it as a standard I am able to assess likely limits for both sexual dimorphism and homogeneity of the fossil hominid groups.

The second section of Chapter 6 involves a Canonical Variates Analysis (CVA). This analysis is carried out using the SPSSX package, DISCRIMINANT, on the Durham University mainframe computer. CVA minimises within-group variation and maximises between-group differences. It is used to examine the interrelationships between a number of groups and to represent these interrelationships graphically in only a few dimensions. The axes of variation are chosen to maximise the separation between the groups, relative to the variation within each of the groups.

The first canonical variate (CV) is that linear combination of the characters which maximises the between group variance. Successive CV's account for smaller and smaller amounts of the total between group variance. In a manner similar to PCA, a number of Variates are chosen which account for the most between-group variance and these CV's can be related back to the original variables to determine if the CV corresponds to some biologically meaningful source of variation. The CV's are chosen such that they account for approximately 90 per cent of the between group variance and CV scores are calculated for each of the specimens in order to represent the relationships between the groups graphically.

In this CV analysis all modern comparators were entered as known groups. Individual fossils were assigned to groups on the basis of the results of the PCA. Fossil specimens were entered as individuals if, in the PCA, they did not consistently cluster with one or more other specimens. This is because CVA can be used to assign new specimens to one or more of the reference groups. Thus CVA will show to which reference group questionable specimens have the closest morphological similarities.

CVA also calculates probabilities of misclassification which can be applied to the reference groups to see how many individuals would be correctly identified by the allocation procedures. The statistical methods and variables included in each analysis are summarised within each section of Chapter 6.

4.4.2 Cladistics

Data and Specimens

The cladistic analyses are carried out following the methodology outlined in Chamberlain and Wood (1987) and Chamberlain (1987). The advantage of using this methodology is that it allows metric traits to be used, the PAUP (Phylogenetic Analysis Using Parsimony) computer program is easy to use, and no prior decisions about the polarity of characters need to be made.

The ingroups include only the more complete fossil specimens and are restricted to those which have variables which can be included in both analyses. Thus if fossils can not be used in both cladistic analyses they are not included in either (see Table 4.04). The outgroup taxa includes the primates used in previous analyses. Two sets of measurements are used: the first set of measurements are chosen to include variables found to be non-variable and non-dimorphic within the extant hominoids; and the second set includes variables known to be variable and dimorphic within hominoids.

Coding of Data

The variables are standardised for size using the equation given in Chamberlain

TABLE 4.04: **Fossil Specimens included in the Cladistic Analyses**

H. erectus	China: Zhoukoudian GI, HI (mandibles)
	Indonesia: Sangiran 17
	Europe: Mauer
	Africa: KNM-ER 730, 3733, 3883, OH 22, BK 67, BL 8518
H. habilis	Koobi Fora: KNM-ER 1470, 1802, 1805, 1813, 3732
	Olduvai: OH 24
	Swartkrans: SK 847
	Sterkfontein: STW 53
A. afarensis	Hadar: A. L. 198.1, 207.13, 266.1, 288.1, 333.45, 333w.60, 400.1, Reconstruction
	Laetoli: LH 4
A. africanus	Sterkfontein: STS 5, 7, 17, 19, 36, 52, 53, 71, STW 73
	Makapansgat: MLD 6, 9, 18, 37/8, 40
A. robustus	Swartkrans: SK 12, 23, 34, 46, 48
	Kromdraai: TM 1517
A. boisei	Koobi Fora: KNM-ER 406, 732, 729, 3230
	Olduvai: OH 5
	Peninj: Peninj 1

and Wood (1987): rai = log(ai) - log(as) - [log(Xi) - log(Xs)] where *ai* is the measurement *a* taken on individual *i*, *as* is the same measurement taken on the 'standard' form *s*, *Xi* is the mean of a set of measurements taken on individual *i*, and *Xs* is the mean of the same set of measurements taken on *s*. Thus rai is the size standardised value for the measurement *a* taken on individual *i*. The measurements for the 'standard' primate were calculated by averaging the dimensions of *H. sapiens*, *Pan*, *Gorilla*, and *Pongo*.

A computer program was devised within the SPSSX package to obtain the dimensions of the 'standard' primate and to compute the above equation and thus obtain values of *rai* for all specimens. These transformed values (*rai*) were then averaged so that each taxon had one value of *rai* per variable. Since these values were of both positive and negative sign they were converted into discrete character states by dividing each *rai* value by an empirically derived constant (.025 for variable traits and .0175 for non-variable traits) and adding 4 units following the methods for 'combination coding' outlined by Sokal and Rohlf (1981). This method results in each character state having a value between 0 and 8 where a value of 4 equals zero, positive values are coded as 5, 6, 7, or 8 according to their size, and negative values are coded as 3, 2, 1, or 0 according to their size. Very large positive or very small negative transformed values that exceed the chosen range of character states are coded as the maximum (8) or minimum (0) value.

The empirical method of 'combination coding' can be explained as follows: the range of values is examined and the more extreme values are 'ignored'. The outliers of the inner range, a range containing the majority of characters, become the maximum and minimum coded values, 0 and 8, and the numbers within that range take on values from 1 to 7. The extreme values of the original range will code as 0 or 8 depending on their magnitude. This method is justified as it maximises the differences between those inner character values.

This can best be understood by the use of an example. Given a set of numbers: 0-5, 40-60, and 95-100, if the outliers (0 and 100) become 0 and 8 the character states would be: 0 0 0 0 0 0 3 3 3 3 4 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 8 8 8 8 8 8 (dividing each number by a constant with the value of 12.5). Notice that four character states are not being utilised because of the absence of data with values from 6-39, 61-94. If the method outlined previously (where 40 and 60 become the outliers since the majority of characters lie within this range) is used these character states are: 0 0 0 0 0 0 0 0 1 1 2 2 2 3 3 4 4 4 5 5 6 6 6 7 7 8 8 8 8 8 8 8 8 (subtracting 40 to get a range from 0 to 20 then dividing each number by a constant with the value of 2.5). Thus this method increases the number of character states utilised such that they describe the majority of characters, teasing out more information from the data set than if the actual outlying values are used. This method works if positive numbers are used but if negative values occur within the data set an additional step must be taken. Given a range of values including negative values, for example -8 to +8, 0 must code as 4 (when the range of coded values is 0 to 8) and to obtain this result (since 0 divided by any number is 0) the numbers are divided by a constant (2 in this case) such that when 4 units are added to them -4 will code as 0, 0 will code as 4, and +4 will code as 8. This method of coding a data set containing negative numbers involves the fewest number of computations. Other methods can be used as long as the final result is the same.

For the variable traits, the range of rai values is -.572 - +.317 with most values (80 %) falling between -.1 - + .1. Dividing by a constant of .025 and adding four units results in character states from 0 to 8 where rai values $< -.1$ code as 0 and those $> +.1$ code as 8.

For non-variable traits, the range of rai values is -.315 - +.109 with the majority (93 %) falling between -.07 - +.07. Dividing by a constant of .0175 and adding four units results in character states from 0 to 8 where rai values $< -.07$ code as 0 and those $> +.07$ code as 8. The variable trait constant (.025) is also used to code the non-variable traits resulting in a second set of character states. These two sets of character states will be used in separate analyses in Chapter 7 in order to assess the coding method.

Construction of Cladograms

Cladograms are computed using the PAUP (Phylogenetic Analysis Using Parsimony) phylogenetic program (Swofford 1985). This program generates unrooted minimum length trees (Wagner trees) which can then be rooted to form cladograms. The use of the branch - and - bound option allows the most parsimonious unrooted tree to be found. The most parsimonious tree is one which has the shortest length and the highest consistency index (CI). The CI is the sum, over all the characters, of the 'range' of each character (equivalent to the minimum length of a tree computed for that character only) divided by the total tree length for all characters (Swofford 1985). The maximum CI value is 1.00.

To root the tree, a hypothetical outgroup is placed as the sister group to the remaining taxa. The ancestral character states are determined using PAUP's MINF algorithm to assign optimal ancestral character states to the great ape morphotype, a morphotype generally agreed by most researchers to be ancestral to the hominid lineage. The MINF optimisation procedure transfers evolutionary steps from the interior branches towards the terminal branches of the cladogram wherever possible. This procedure minimises the possibility that internal nodes of the cladogram will be defined by an arbitrary choice of derived character states.

The optimisation option is used to find the assignments of characters for the outgroup node that are the most parsimonious according to the outgroup resolution. The outgroup consists of *H. sapiens*, *Pan*, *Gorilla*, and *Pongo*. Three topologies are examined: one with *H. sapiens* and *Pan* sharing a common ancestor with *Gorilla* as the sister group to that ancestor (*Pongo* being used to root the cladogram); one with *Pan* and *Gorilla* sharing a common ancestor and *H. sapiens* as a sister group to that ancestor; and one with *H. sapiens* and *Gorilla* sharing a common ancestor with *Pan* as the sister group to that ancestor. In all three topologies the length of each tree and its consistency index (CI) are noted as well as the ancestral states at the outgroup node representing the ancestor of *H. sapiens*, *Pan*, and *Gorilla*. Since the relationship between the African apes and *H. sapiens* is not resolved, the predominent states method (Maddison *et al.* 1984) is used whereby the most common state among the three scenarios at the outgroup node is taken to be the ancestral state. Thus if the first topology yields a character state of 2, the second 3, and the third 2, then 2 is assigned to the character state of the hypothetical ancestor for that measurement. An alternative method of assigning ancestral character states would be to choose ancestral states from the topology which produces the most parsimonious cladogram (ie. shortest tree with highest value of CI). The results of using both methods of determining ancestral states are presented in Chapter 7.

Thus the most parsimonious unrooted tree can be rooted to form a cladogram using the hypothetical outgroup. The results of these analyses are presented and discussed in Chapter 7.

CHAPTER 5: UNIVARIATE ANALYSIS 1: WITHIN-SPECIES VARIATION

5.1 Introduction

This chapter involves an assessment of within- and between-species variability in individual characters using raw data. Patterns of cranial variation are examined within *H. sapiens*, *Pan*, *Gorilla*, and *Pongo* to provide comparative data for the study of within- and between-species variability of the fossil samples. The purpose of this chapter is to isolate characters that may be useful for either discriminating between sexes or testing the homogeneity of the fossil groups and which thus address first two aims of this thesis.

Chapter 5 is divided into two sections. In the first, Univariate Analysis 1, an assessment of within-species variation is made. Each region of the skull (mandible, palate, base, vault, face) as well as the overall effect on the cranium, are examined within each of the modern and fossil species to determine if any patterns of sexual dimorphism exist in variance and or in mean values. This preliminary analysis is necessary to determine the pattern of variation within each sample group of modern comparators and to eliminate characters which are too variable to be use in the examination of the fossil samples.

Section two, Univariate Analysis 2, compares patterns of variation between species in order to determine if, within the modern hominoids, there exists 1) a common pattern of sexual dimorphism which can then be used to assess fossil sexual dimorphism; and 2) characters of high phyletic valence which can be used to test the homogeneity of the fossil groups. The results of this section are then applied to the fossil groups in sections 5.21 to 5.26.

5.2 Univariate Statistical Methods

An SPSSX program was used to calculate the mean, standard deviation, and the standard error of the sample statistics for each sex of each modern species for each variable and the mean and standard deviation only for the fossil hominid species. This program also calculated the F value (variance), T value (mean, 2-tailed probability) when comparing the variances and means of the sexes of each modern species for each variable. The formula Female Mean/ Male Mean x 100 was used to calculate percentage sexual dimorphism for the modern comparators only. The coefficient of variation (CV) was calculated for each sex (modern species only) and for each species (fossil and modern) using the formula: standard deviation multiplied by one hundred and then divided by the mean.

When confidence intervals for the CV are discussed in Univariate Analysis 2, they are computed using the formula: CV ± the standard error of the CV multiplied by the t value (p=.05) at the appropriate degree of freedom. The confidence limits around a given CV can be used as a reliability indicator of that CV. Since the CV's used in this study are sample estimates, the confidence limits indicate how likely this estimate is to be close to that of the true population value of CV. The use of 95 per cent confidence limits indicates that there is 95 per cent probability that the population CV lies within the given sample CV's confidence interval. The formulae for the CV and its confidence limits were found in Sokal and Rohlf (1981).

5.3 Homo sapiens

5.3.1 Mandible

Sex differences in variance

There was no sexual difference in variance (F value) for the 12 variables (p= 0.05 or less) (see table 5.01). The coefficient of variation for the species ranges from 5.45 (M3) to 14.46 (M5- symphyseal height) (see table 5.02). Male values range from 5.04 (M5) to 14.41 (M12) and males are more variable than females in all but two characters (M4 and M6). Males have a higher value of CV than does the species in two traits (M8- internal breadth and M12- arcadal length). Female values range from 3.61 (M3) to 10.60 (M12). Thus males values of CV are higher than the majority of those of females though neither sex is very variable in mandibular characters and there are no significant differences between the sexes in terms of variance.

Sex differences in mean values

There was a significant difference between the means (T value) of the sexes at the 0.05 % level or less for ten of the twelve mandibular characters (M1 to M7, M9 to M11) (see table 5.01). Percentage sexual dimorphism for the mandible has a range of 81.2 (M10) to 94.9 % (M12) (see table 5.03). For M10 (depth of the corpus at M1) there is some overlap of the ranges of males and females. For M12 (arcadal length) the ranges totally overlap with males more variable than females. The mean percentage sexual dimorphism for the mandible is 88.7 %. The difference between male and female mandibles seems to be one of size except for M8 (internal breadth) and M12 where male values overlap the range of female values.

TABLE 5.01: HOMO SAPIENS: SUMMARY STATISTICS: MANDIBLE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
M1	M	9	10.7789	0.906	0.302	1.65	0.494	4.51	16	0.000
	F	9	9.0544	0.705	0.235					
M2	M	9	4.6722	0.235	0.078	2.03	0.312	3.85	17	0.001
	F	10	4.3160	0.165	0.052					
M3	M	10	10.4100	0.532	0.168	2.28	0.261	3.04	17	0.007
	F	9	9.7722	0.353	0.118					
M4	M	10	3.4310	0.269	0.085	1.06	0.940	2.57	17	0.020
	F	9	3.1178	0.260	0.087					
M5	M	9	3.3311	0.353	0.118	2.02	0.316	4.50	17	0.000
	F	10	2.7070	0.248	0.078					
M6	M	8	6.8425	0.535	0.189	1.17	0.853	3.36	15	0.004
	F	9	5.9322	0.577	0.192					
M7	M	10	1.6170	0.174	0.055	1.65	0.467	2.19	18	0.042
	F	10	1.4640	0.136	0.043					
M8	M	9	5.6633	0.610	0.203	1.89	0.363	1.84	17	0.083
	F	10	5.2160	0.444	0.140					
M9	M	9	7.1011	0.414	0.138	1.83	0.386	2.68	17	0.016
	F	10	6.6570	0.306	0.097					
M10	M	10	3.0640	0.265	0.084	1.89	0.358	5.57	18	0.000
	F	10	2.4870	0.193	0.061					
M11	M	10	2.8840	0.250	0.079	2.49	0.213	5.09	17	0.000
	F	9	2.3889	0.158	0.053					
M12	M	9	4.4411	0.640	0.213	2.05	0.304	0.90	17	0.380
	F	10	4.2150	0.447	0.141					

* value for males and females

TABLE 5.02: HOMINOIDS: COEFFICIENT OF VARIATION: MANDIBLE

SP	SEX	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
HS		11.96	5.97	5.45	9.24	14.46	11.24	11.12	10.37	6.09	13.40	12.33	12.57
HS	M	8.41	5.04	5.11	7.83	10.58	7.82	10.79	10.77	5.83	8.64	8.65	14.41
HS	F	7.79	3.83	3.61	8.35	9.17	9.73	9.28	8.52	4.60	7.75	6.62	10.60
PA		10.34	7.27	6.81	9.75	12.28	7.20	12.02	7.59	5.37	9.28	9.04	6.26
PA	M	7.51	6.46	4.75	9.21	9.82	5.98	13.44	4.45	3.32	7.99	8.16	6.45
PA	F	11.13	8.33	7.21	5.06	11.89	5.17	11.15	9.80	7.02	9.30	8.95	6.37
GO		13.95	6.79	11.53	17.15	17.43	15.52	9.46	11.10	4.18	10.51	12.83	9.05
GO	M	8.72	4.52	6.61	8.25	12.74	7.90	8.38	11.81	2.51	5.28	6.45	6.24
GO	F	9.46	5.57	5.61	5.49	8.35	7.45	7.75	10.30	4.70	8.44	9.69	3.93
PO		14.04	12.31	12.12	15.29	14.42	12.92	12.09	6.86	6.45	11.32	13.96	8.01
PO	M	13.11	12.73	8.73	11.23	10.78	10.96	13.59	8.40	4.80	8.51	11.27	3.79
PO	F	7.04	5.52	5.02	8.32	11.64	7.14	8.12	4.22	3.91	9.04	10.72	4.56

TABLE 5.03: HOMINOIDS: PERCENTAGE SEXUAL DIMORPHISM: MANDIBLE

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	MEAN
HS	84.0	92.4	93.9	90.9	81.3	86.7	90.5	92.1	93.8	81.2	82.8	94.9	88.7
PA	90.8	100.7	93.5	88.5	88.3	91.3	101.0	96.1	98.5	92.6	93.3	98.9	94.5
GO	80.9	91.2	82.6	73.7	76.8	76.7	90.3	95.3	96.0	85.3	81.9	86.6	84.8
PO	83.9	87.0	82.8	79.7	83.1	84.0	91.3	96.1	91.1	86.5	84.1	87.4	86.4

5.3.2 Palate

Sex differences in variance

There was a significant difference between the variances of the sexes for one variable (P3- maxillo-alveolar length) at the 5 % level (see table 5.04). The values for the coefficient of variation (see table 5.05) vary between 5.67 (P6) to 9.54 (P2) excluding 2 variables P7 (CV=23.18) and P8 (CV=20.16) (Palatal depth at M1 and M3). The high value of CV may be due to alveolar border damage and the fact that for small measurements there is greater room for measurement error. Male values range from 5.18 (P6) to 8.73 (P3) excluding P7 and P8. Males are more variable than females in all traits except P2 (internal breadth). Males have a larger value of CV than does the species for three traits (P3, P5, P7). Female values range from 3.07 (P6) to 8.87 (P2) excluding values for P7 and P8. Males are almost two times more variable for P3 than females which accounts for there being a significant difference between the sexes in variance, though neither sex has a high value of CV for this trait. Thus apart from variables P7 and P8, *H. sapiens* is not variable in these palatal measurements.

Sex differences in mean values

Six of the nine variable means of the sexes were significantly different at the 5 % level or less (P1 to P4, P6, P9) (see table 5.04). Percentage sexual dimorphism for the palate has a range of 83.1 (P8) to 100.9 (P5) % (see table 5.06). For P8 (palatal depth at M3) there is a complete overlap of the ranges of male and female values for this variable but since the measurement is small, the difference in the means is magnified and for P5 (arcadal length) both sexes are variable and the ranges overlap. The mean percentage sexual dimorphism for the palate is 91 %. Thus size accounts for most of the difference between males and females.

5.3.3 Base

Sex differences in variance

None of the twenty-four variables showed a sex difference in variance (see table 5.07). B23 (articular eminence height) and B24 (post-glenoid process height) were difficult to measure while trying to orient the skull in the Frankfurt Horizontal and this factor may be the cause of the high CV values for these traits (see table 5.08). Male values range from 4.80 (B18) to 16.39 (B11- length along the petrous temporal to the centre of the carotid canal) excluding values for B23 and B24. Males are more variable than females in 7 cases (B1, B11, B15, B19, B20, B22, B24) and males are

TABLE 5.04: HOMO SAPIENS: SUMMARY STATISTICS: PALATE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
P1	M	9	4.6900	0.357	0.119	1.61	0.494	2.76	17	0.014
	F	10	4.2860	0.281	0.089					
P2	M	8	4.3087	0.309	0.109	1.24	0.794	2.77	16	0.014
	F	10	3.8760	0.344	0.109					
P3	M	8	5.5987	0.489	0.173	4.77	0.043	2.76	15	0.015
	F	9	5.1000	0.224	0.075					
P4	M	6	6.5083	0.358	0.146	1.86	0.394	3.78	14	0.002
	F	10	5.9220	0.263	0.083					
P5	M	7	4.9057	0.361	0.136	1.45	0.663	-0.25	12	0.807
	F	7	4.9500	0.299	0.113					
P6	M	5	6.5800	0.341	0.152	3.33	0.183	3.28	10	0.008
	F	7	6.0814	0.187	0.071					
P7	M	9	1.2711	0.321	0.107	1.97	0.332	1.11	17	0.284
	F	10	1.1310	0.228	0.072					
P8	M	9	1.3222	0.243	0.081	1.48	0.619	2.05	15	0.058
	F	8	1.0987	0.200	0.071					
P9	M	10	2.5660	0.205	0.065	2.04	0.305	3.26	18	0.004
	F	10	2.3080	0.144	0.045					
	*	value	for	males	and	females				

TABLE 5.05: HOMINOIDS: COEFFICIENT OF VARIATION: PALATE

SP	SEX	P1	P2	P3	P4	P5	P6	P7	P8	P9
HS		8.33	9.54	8.28	6.71	6.48	5.67	23.18	20.16	8.92
HS	M	7.61	7.16	8.73	5.50	7.35	5.18	25.24	18.38	8.00
HS	F	6.57	8.87	4.38	4.43	6.05	3.07	20.20	18.19	6.23
PA		8.72	6.93	6.98	5.68	6.22	5.31	11.56	14.93	8.45
PA	M	8.17	4.81	5.18	4.09	7.75	4.04	13.04	12.23	7.81
PA	F	7.91	8.84	8.32	7.10	4.58	6.57	9.05	16.06	9.36
GO		13.55	9.08	11.52	6.75	9.76	6.70	18.22	13.87	13.32
GO	M	9.42	6.75	7.31	3.79	6.46	3.74	14.03	10.67	13.91
GO	F	6.45	7.20	4.71	5.80	4.01	5.35	20.67	16.15	10.93
PO		11.27	10.92	9.05	8.27	7.55	7.88	26.43	22.93	13.50
PO	M	7.05	9.88	5.77	6.82	3.64	5.88	22.33	15.11	13.50
PO	F	6.12	7.50	4.96	4.36	4.36	4.00	23.50	16.59	6.61

TABLE 5.06: HOMINOIDS: PERCENTAGE SEXUAL DIMORPHISM: PALATE

	P1	P2	P3	P4	P5	P6	P7	P8	P9	MEAN
HS	91.4	90.0	91.1	91.0	100.9	92.4	89.0	83.1	90.0	91.0
PA	92.8	100.3	96.2	101.0	98.9	100.1	93.7	89.1	101.8	97.1
GO	81.0	88.9	82.8	91.0	85.3	90.7	87.1	91.5	90.6	87.7
PO	83.6	87.9	86.7	89.0	88.1	88.8	75.9	71.6	85.6	84.1

TABLE 5.07: HOMO SAPIENS: SUMMARY STATISTICS: BASE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B1	M	10	3.5540	0.382	0.121	1.22	0.808	0.96	16	0.349
	F	8	3.3862	0.346	0.122					
B2	M	10	3.0100	0.195	0.062	1.81	0.395	0.96	17	0.350
	F	9	2.9089	0.262	0.087					
B3	M	10	10.7260	0.560	0.177	1.35	0.666	2.71	18	0.014
	F	10	9.9920	0.649	0.205					
B4	M	10	8.9080	0.443	0.140	1.80	0.392	2.79	18	0.012
	F	10	8.2540	0.595	0.188					
B5	M	10	8.3910	0.461	0.146	1.85	0.375	2.67	18	0.015
	F	10	7.7330	0.627	0.198					
B6	M	10	6.2030	0.506	0.160	1.08	0.914	1.68	18	0.110
	F	10	5.8160	0.525	0.166					
B7	M	10	3.6060	0.311	0.098	1.29	0.711	2.49	18	0.023
	F	10	3.2350	0.353	0.112					
B8	M	10	5.2410	0.358	0.113	1.03	0.963	1.72	18	0.102
	F	10	4.9680	0.352	0.111					
B9	M	10	6.8670	0.407	0.129	2.05	0.301	0.36	18	0.726
	F	10	6.7870	0.583	0.184					
B10	M	10	2.6510	0.219	0.069	1.25	0.742	2.24	18	0.038
	F	10	2.4180	0.245	0.078					
B11	M	10	1.9670	0.322	0.102	3.44	0.080	0.95	18	0.355
	F	10	1.8570	0.174	0.055					
B12	M	10	5.2260	0.342	0.108	1.15	0.840	2.59	18	0.018
	F	10	4.8150	0.367	0.116					

* value for males and females

TABLE 5.07: HOMO SAPIENS: SUMMARY STATISTICS: BASE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B13	M	10	2.9380	0.284	0.090	1.67	0.457	1.66	18	0.115
	F	10	2.6950	0.367	0.116					
B14	M	10	4.9400	0.418	0.132	1.18	0.824	3.28	17	0.004
	F	9	4.3333	0.384	0.128					
B15	M	10	2.5180	0.326	0.103	1.82	0.412	2.18	17	0.043
	F	9	2.2278	0.242	0.081					
B16	M	10	11.6280	0.591	0.187	1.80	0.395	1.13	18	0.272
	F	10	11.2740	0.792	0.250					
B17	M	10	13.3890	0.779	0.246	2.74	0.149	2.42	18	0.027
	F	10	12.2380	1.290	0.408					
B18	M	10	10.7590	0.516	0.163	1.91	0.350	2.26	18	0.037
	F	10	10.1310	0.713	0.226					
B19	M	10	6.1470	0.655	0.207	2.34	0.222	1.61	18	0.124
	F	10	5.7480	0.428	0.135					
B20	M	10	8.8100	1.130	0.357	1.01	0.990	-0.10	18	0.922
	F	10	8.8600	1.135	0.359					
B21	M	9	3.1144	0.170	0.057	3.07	0.134	1.75	16	0.100
	F	9	2.9144	0.298	0.099					
B22	M	9	4.5678	0.376	0.125	1.27	0.741	2.23	16	0.040
	F	9	4.1944	0.333	0.111					
B23	M	10	0.5930	0.113	0.036	1.61	0.491	1.98	18	0.063
	F	10	0.4790	0.143	0.045					
B24	M	10	0.8080	0.220	0.070	2.01	0.313	2.29	18	0.034
	F	10	0.6130	0.155	0.049					

* value for males and females

TABLE 5.08: HOMINOIDS: COEFFICIENT OF VARIATION: BASE

SP	SEX	B1	B2	B3	B4	B5	B6
HS		10.52	7.72	6.76	7.12	7.85	8.97
HS	M	10.76	6.48	5.22	4.97	5.50	8.15
HS	F	10.21	9.02	6.50	7.20	8.10	9.02
PA		11.02	9.31	6.64	5.68	6.06	6.47
PA	M	10.37	6.76	5.17	5.23	5.22	6.56
PA	F	11.70	11.64	6.63	5.28	6.55	5.57
GO		7.44	10.31	10.18	7.85	8.16	10.87
GO	M	6.21	4.90	5.36	6.51	4.45	8.27
GO	F	5.88	9.07	4.11	4.58	7.97	7.54
PO		11.76	9.16	9.63	7.16	8.81	9.48
PO	M	11.82	6.75	7.91	7.03	8.09	9.15
PO	F	12.13	11.74	5.59	5.59	7.29	5.25

SP	SEX	B7	B8	B9	B10	B11	B12
HS		10.98	7.30	7.19	10.10	13.51	8.06
HS	M	8.62	6.82	5.93	8.26	16.39	6.55
HS	F	10.91	7.08	8.58	10.14	9.35	7.62
PA		6.71	6.47	5.38	12.36	7.93	8.94
PA	M	6.72	4.83	3.51	10.31	8.56	10.52
PA	F	6.47	8.06	6.98	11.58	6.60	6.60
GO		11.85	7.64	7.02	13.47	11.71	14.12
GO	M	7.70	7.63	6.34	9.95	8.28	9.73
GO	F	8.93	6.44	5.33	9.69	10.84	6.75
PO		8.42	8.10	9.60	11.03	11.15	13.46
PO	M	7.36	7.19	10.34	9.31	8.39	9.36
PO	F	8.65	6.20	8.07	8.74	8.08	9.26

TABLE 5.08: HOMINOIDS: COEFFICIENT OF VARIATION: BASE CONT'D

SP	SEX	B13	B14	B15	B16	B17	B18
HS		12.18	10.74	13.37	6.15	9.31	6.57
HS	M	9.67	8.45	12.95	5.08	5.82	4.80
HS	F	13.62	8.86	10.85	7.03	10.54	7.04
PA		12.84	5.18	12.09	7.75	5.61	8.82
PA	M	14.09	4.36	7.90	9.41	4.40	4.94
PA	F	9.55	5.77	13.90	5.54	4.73	11.55
GO		15.78	15.58	15.16	16.40	11.86	10.31
GO	M	8.49	10.65	7.53	7.19	3.24	5.85
GO	F	10.26	9.62	13.59	10.06	6.31	5.85
PO		16.70	11.98	11.84	13.26	11.19	9.88
PO	M	14.36	10.57	12.46	10.18	9.44	9.14
PO	F	10.41	4.54	7.09	7.94	6.52	5.81

SP	SEX	B19	B20	B21	B22	B23	B24
HS		9.69	12.48	8.53	9.00	25.81	29.66
HS	M	10.66	12.82	5.47	8.22	19.03	27.25
HS	F	7.45	12.80	10.23	7.94	29.86	25.33
PA		14.95	19.21	10.69	7.20	63.37	22.83
PA	M	11.79	22.69	5.98	3.81	67.75	19.05
PA	F	16.68	16.02	14.28	9.53	42.69	27.26
GO		12.68	21.92	15.48	14.15	50.47	20.08
GO	M	7.09	9.45	8.59	8.91	46.27	24.29
GO	F	8.38	9.07	11.96	6.63	41.88	14.96
PO		10.37	14.40	14.98	14.30	25.57	37.14
PO	M	10.44	15.91	12.40	11.93	25.18	42.44
PO	F	5.74	3.60	6.44	5.27	12.91	30.98

more variable than is the species in four cases (B1, B11, B19, B20). Female values range from 6.50 (B3) to 12.80 (B20) excluding B23 and B24. Thus males are variable in characters relating to the kyphosis of the cranial base as well as in the nuchal region and females are more variable than males in the majority of variables measured but overall, *H. sapiens* has low values of CV for this region.

Sex differences in mean values

There was a significant difference between the means of the sexes for 12 variables at the 5 % or less level (B3, B4, B5, B7, B10, B12, B14, B15, B17, B18, B22, B24) (see table 5.07). Percentage sexual dimorphism for the basicranium has a range of 75.9 (B24) to 100.6 (B20) % (see table 5.09). For B24 (post-glenoid process height) there is a large overlap in the ranges of values for males and females but because it is a small measurement the difference between the means is magnified. For B20 (lateral nuchal crest arc) both sexes are variable for this character and their ranges of values overlap. The mean percentage sexual dimorphism for the basicranium is 92 %. The base of *H. sapiens* males and females can be distinguished mainly on the basis of size differences in width measurements, however B12, B14, B15, and B22 are all related to the kyphosis of the cranium with males generally larger than females although the range of values of the two sexes overlap.

5.3.4 Vault

Sex differences in variance

There was no significant difference between the sexes in the variance of any variable (p=0.05 or less) (see table 5.10) and values of CV for the species range from 3.62 (V21) to 17.70 (V24) (see table 5.11). V24 (mastoid width) is variable for males and females while V23 (mastoid length) and V12 - 14 (inion arc, nuchal chord and arc) are variable for females which contribute most to species variability for these characters. Male values range from 2.57 (V21) to 14.59 (V24) with males being more variable than females in 7 traits (V1, V3, V4, V10, V15, V19, V20) and are more variable than the species in five traits (V3, V10, V15, V19, V20). These measurements may all be functionally correlated so when the temporal muscles are robust (V15) so too are the maxilla (V19, V20) and the frontal bone (V1, V3, V4, V10) to absorb stress generated during chewing. Female values range from 3.31 (V19) to 19.36 (V13), are more variable than males in 17 traits, and are more variable than the species in 8 traits (V7, V12, V13, V14, V17, V21, V23, V24). Most of these measurements are ones of length and may be caused by size differences within this sex. Thus although there is no significant difference between the variance of the sexes, females have higher

TABLE 5.09: HOMINOIDS: PERCENTAGE SEXUAL DIMORPHISM: BASE

	B1	B2	B3	B4	B5	B6	B7	B8	B9
HS	95.3	96.6	93.2	92.7	92.2	93.8	89.7	94.8	98.8
PA	95.2	97.3	93.7	95.3	96.3	95.2	96.3	100.3	99.8
GO	91.5	86.2	83.9	89.8	90.0	86.2	84.4	93.9	92.4
PO	96.9	99.3	87.6	93.4	91.5	89.3	93.9	91.2	94.2
	B10	B11	B12	B13	B14	B15	B16	B17	B18
HS	91.2	94.4	92.1	91.7	87.7	88.5	97.0	91.3	94.2
PA	88.4	95.1	95.6	91.1	97.1	89.6	96.9	93.5	95.5
GO	83.2	86.9	80.2	77.6	79.2	80.2	75.7	80.7	84.6
PO	87.9	86.0	82.4	80.8	84.6	88.9	86.8	86.0	88.5
	B19	B20	B21	B22	B23	B24	MEAN		
HS	93.5	100.6	93.6	91.8	80.8	75.9	91.2		
PA	89.5	98.1	100.7	96.6	68.2	95.7	94.2		
GO	81.8	67.8	79.1	79.5	63.4	94.7	83.0		
PO	89.0	85.6	80.8	81.3	75.5	90.3	88.0		

TABLE 5.10: HOMO SAPIENS: SUMMARY STATISTICS: VAULT

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V1	M	10	12.4350	0.591	0.187	1.82	0.386	2.62	18	0.017
	F	10	11.8250	0.438	0.138					
V2	M	10	14.4850	0.604	0.191	1.10	0.892	2.03	18	0.058
	F	10	13.9250	0.633	0.200					
V3	M	10	12.8600	0.789	0.250	1.67	0.458	1.55	18	0.138
	F	10	12.3700	0.611	0.193					
V4	M	10	11.2510	0.504	0.160	1.48	0.568	2.32	18	0.032
	F	10	10.7710	0.415	0.131					
V5	M	10	13.3600	0.810	0.256	1.09	0.903	1.70	18	0.106
	F	10	12.7300	0.845	0.267					
V6	M	10	11.8140	0.692	0.219	1.01	0.990	1.67	18	0.112
	F	10	11.2980	0.689	0.218					
V7	M	10	11.8600	0.578	0.183	2.60	0.171	0.43	18	0.670
	F	10	11.7100	0.931	0.295					
V8	M	10	9.7630	0.527	0.167	1.03	0.962	1.97	18	0.064
	F	10	9.2950	0.536	0.169					
V9	M	10	13.3950	0.430	0.136	1.28	0.715	4.13	18	0.001
	F	10	12.5450	0.488	0.154					
V10	M	10	9.4850	0.656	0.208	2.22	0.250	1.35	18	0.194
	F	10	9.1480	0.440	0.139					
V11	M	10	6.4920	0.713	0.226	1.15	0.841	0.73	18	0.475
	F	10	6.2670	0.666	0.211					
V12	M	10	7.0000	0.783	0.248	2.07	0.293	0.43	18	0.675
	F	10	6.8150	1.127	0.357					

* value for males and females

TABLE 5.10: HOMO SAPIENS: SUMMARY STATISTICS: VAULT CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V13	M	10	4.7560	0.547	0.173	2.71	0.154	0.32	18	0.749
	F	10	4.6480	0.900	0.285					
V14	M	10	4.9100	0.549	0.173	2.74	0.149	-0.03	18	0.977
	F	10	4.9200	0.909	0.287					
V15	M	9	8.2989	0.948	0.316	1.34	0.669	1.27	17	0.222
	F	10	7.7850	0.819	0.259					
V16	M	9	25.5444	2.474	0.825	1.32	0.704	2.87	17	0.011
	F	10	22.0200	2.845	0.900					
V17	M	10	12.0880	0.406	0.128	3.72	0.064	2.66	18	0.016
	F	10	11.3450	0.783	0.248					
V18	M	10	9.4820	0.367	0.116	1.02	0.978	2.30	18	0.034
	F	10	9.1070	0.363	0.115					
V19	M	10	8.6560	0.430	0.136	2.48	0.192	2.47	18	0.024
	F	10	8.2580	0.273	0.086					
V20	M	10	7.2970	0.434	0.137	2.17	0.263	3.63	18	0.002
	F	10	6.6940	0.295	0.093					
V21	M	10	18.6650	0.479	0.151	1.93	0.340	2.62	18	0.017
	F	10	17.9850	0.666	0.211					
V22	M	10	12.8070	0.431	0.136	1.55	0.524	2.71	18	0.014
	F	10	12.2180	0.536	0.170					
V23	M	10	2.9060	0.315	0.100	1.99	0.319	0.17	18	0.864
	F	10	2.8760	0.446	0.141					
V24	M	10	2.4850	0.362	0.115	1.11	0.880	2.19	18	0.042
	F	10	2.1210	0.382	0.121					

* value for males and females

TABLE 5.11: HOMINOIDS: COEFFICIENT OF VARIATION: VAULT

SP	SEX	V1	V2	V3	V4	V5	V6	V7	V8	V9	V10	V11	V12
HS		4.91	4.69	5.80	4.65	6.65	6.25	6.43	5.98	4.82	6.13	10.68	13.75
HS	M	4.75	4.17	6.14	4.48	6.06	5.86	4.87	5.40	3.21	6.92	10.99	11.19
HS	F	3.70	4.54	4.94	3.85	6.64	6.10	7.95	5.76	3.89	4.81	10.63	16.54
PA		4.25	4.22	6.10	5.64	9.31	8.90	9.20	7.95	4.12	7.99	24.68	24.22
PA	M	4.93	4.08	5.46	5.25	6.82	7.08	10.40	9.77	3.58	9.37	23.84	22.85
PA	F	3.71	4.48	5.67	5.10	11.65	10.82	8.00	6.03	4.58	6.06	26.23	26.65
GO		5.95	6.19	15.84	13.07	15.00	14.74	28.21	9.55	7.02	8.63	46.76	54.80
GO	M	7.38	7.62	9.62	9.16	13.98	12.93	35.01	8.99	5.29	8.73	31.59	27.37
GO	F	3.44	4.52	11.77	11.41	16.72	17.04	11.37	6.75	4.10	8.30	30.69	28.40
PO		6.87	6.01	10.15	9.10	7.04	6.66	11.55	11.62	6.90	6.74	30.76	32.67
PO	M	6.05	6.92	10.69	8.87	7.03	6.18	11.42	11.16	7.35	5.17	24.20	26.44
PO	F	7.24	4.15	9.20	8.59	4.87	4.63	8.51	9.76	4.53	7.98	37.81	39.57

TABLE 5.11: HOMINOIDS: COEFFICIENT OF VARIATION: VAULT CONT'D

SP	SEX	V13	V14	V15	V16	V17	V18
HS		15.46	14.87	11.17	13.37	6.12	4.35
HS	M	11.50	11.17	11.42	9.68	3.36	3.87
HS	F	19.36	18.47	10.52	12.92	6.90	3.99
PA		16.62	17.05	10.70	12.35	6.14	5.17
PA	M	18.88	19.03	8.83	9.23	4.54	4.91
PA	F	13.86	13.53	10.52	11.90	6.39	4.94
GO		28.31	28.89	14.52	18.91	9.80	9.70
GO	M	18.97	19.25	5.13	7.32	3.97	7.20
GO	F	7.76	7.75	2.65	6.41	4.49	3.58
PO		15.21	14.90	16.18	15.76	10.78	8.71
PO	M	17.98	14.34	14.86	13.94	9.10	8.38
PO	F	8.84	12.74	7.20	8.45	7.19	5.12

SP	SEX	V19	V20	V21	V22	V23	V24
HS		4.80	6.80	3.62	4.49	13.01	17.70
HS	M	4.97	5.95	2.57	3.36	10.86	14.59
HS	F	3.31	4.40	3.70	4.39	15.49	17.99
PA		5.50	6.72	4.64	4.57	31.00	36.39
PA	M	5.34	6.04	4.02	3.85	22.95	31.53
PA	F	4.60	5.12	4.68	4.23	38.90	41.28
GO		10.68	14.78	13.96	9.94	27.30	22.04
GO	M	7.70	8.84	8.52	2.72	22.00	12.18
GO	F	4.31	3.66	4.05	4.57	25.40	20.55
PO		9.64	13.58	5.61	10.42	31.34	21.49
PO	M	8.10	11.28	5.11	8.84	28.26	13.03
PO	F	5.94	8.19	2.42	6.31	32.67	26.07

values of CV than males in the majority of characters measured.

Sex differences in mean values

The means of the sexes for 11 traits were significantly different at the 5 % level or less (V1, V4, V9, V16 - 22, V24) (see table 5.10) and percentage sexual dimorphism for the vault has a range of 85.3 (V24) to 100.2 (V14) (see table 5.12). V24 (mastoid width) is a variable character for both males and females and, although the ranges of values for the sexes overlap, male values tend to be larger than female values. The sexes are both variable for V14 (nuchal arc) and the ranges overlap. The mean percentage sexual dimorphism for the vault is 95.2 % and most of the differences between the sexes are due to overall size differences with males being generally larger and more robust than females. Another difference arises in maxilla projection with males having more prominent cheekbones (V18 - 20) which is not suprising since measurements of the cranial base related to kyphosis are also variable and cranial base kyphosis is related to facial projection.

5.3.5 Face

Sex differences in variance

There was no significant difference between the sexes in the variance of any variable (p=0.05 or less) (see table 5.13) and values of CV for the species have a range of 4.09 (F4) to 14.33 (F20) excluding four variables (see table 5.14). F5, glabella projection (CV=39.58), is a small measurement so any error in measurement would magnify the value of CV and the variability of F16 (distance from the root of the zygomatic to the alveolar margin) (CV=28.89) could have been caused by the difficulty in exactly identifying where the root of the zygomatic began and/ or alveolar damage. The measurements F26 and F27 were taken at the zygomatic suture which is not necessarily at the widest point and can vary in position among different individuals which may account for the high values of CV for these two traits. Male values range from 3.29 (F6) to 12.96 (F10), males are more variable than females in eight traits (F2, F4, F8, F10, F12, F22, F25, F27) (width, length and height measurements possibly related to prognathism), and males are more variable than the species in four cases (F2, F10, F22, F25). Female values range from 3.96 (F8) to 11.79 (F20) and females are more variable than the species in 8 cases (F3, F5, F9, F11, F17, F18, F21, F26). Variables F3 and F18 are interconnected in that the size of F3 (orbit breadth) may affect the size of F18 (superior malar length) but most of the other variables are measures of width. Females have higher values of CV than males in many variables but there is no statistically significant sexual difference in variances.

TABLE 5.12: HOMINOIDS: PERCENTAGE SEXUAL DIMORPHISM: VAULT

	V1	V2	V3	V4	V5	V6	V7	V8	V9
HS	95.1	96.1	96.2	95.7	95.3	95.6	98.7	95.2	93.6
PA	99.7	98.8	94.7	95.2	100.5	99.9	97.0	98.8	98.0
GO	96.6	98.2	79.0	84.7	98.3	97.1	83.4	89.8	90.3
PO	95.6	95.9	94.7	93.9	92.9	92.6	89.3	90.0	93.7
	V10	V11	V12	V13	V14	V15	V16	V17	V18
HS	96.4	96.5	97.4	97.7	100.2	93.8	86.2	93.8	96.0
PA	96.3	105.8	98.7	93.8	90.9	90.5	87.3	94.3	96.3
GO	95.5	50.3	37.8	63.5	62.8	76.2	70.7	84.0	85.9
PO	96.6	97.3	88.1	90.1	87.8	81.1	81.5	87.1	90.2
	V19	V20	V21	V22	V23	V24	MEAN		
HS	95.4	91.7	96.4	95.4	99.0	85.3	95.1		
PA	95.1	92.7	96.4	95.6	86.1	82.3	95.2		
GO	84.6	77.6	78.9	83.4	74.7	73.3	79.9		
PO	88.0	83.4	92.6	87.1	81.0	82.0	89.7		

TABLE 5.13: HOMO SAPIENS: SUMMARY STATISTICS: FACE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F1	M	10	10.1870	0.373	0.118	1.24	0.754	2.74	18	0.013
	F	10	9.7040	0.415	0.131					
F2	M	10	2.3200	0.234	0.074	2.10	0.285	0.54	18	0.593
	F	10	2.2710	0.162	0.051					
F3	M	10	4.0200	0.213	0.067	1.45	0.587	1.50	18	0.151
	F	10	3.8620	0.256	0.081					
F4	M	10	3.3610	0.137	0.043	1.00	0.999	-1.29	18	0.213
	F	10	3.4400	0.137	0.043					
F5	M	10	0.3160	0.077	0.024	1.27	0.724	3.30	18	0.004
	F	10	0.1950	0.087	0.027					
F6	M	10	11.9260	0.392	0.124	1.36	0.656	4.81	18	0.000
	F	10	11.0090	0.457	0.145					
F7	M	9	13.2733	0.616	0.205	1.66	0.488	3.25	17	0.005
	F	10	12.2050	0.793	0.251					
F8	M	10	10.3600	0.391	0.124	1.16	0.831	3.04	18	0.007
	F	10	9.8470	0.363	0.115					
F9	M	10	9.5400	0.335	0.106	3.86	0.057	1.36	18	0.190
	F	10	9.2220	0.658	0.208					
F10	M	10	2.4370	0.316	0.100	1.73	0.425	0.77	18	0.449
	F	10	2.3400	0.240	0.076					
F11	M	10	5.3530	0.335	0.106	1.05	0.945	1.16	18	0.260
	F	10	5.1770	0.343	0.108					
F12	M	10	6.9870	0.466	0.147	1.37	0.647	3.02	18	0.007
	F	10	6.4030	0.398	0.126					
F13	M	10	5.3270	0.308	0.097	1.07	0.921	2.88	18	0.010
	F	10	4.9240	0.319	0.101					

* value for males and females

TABLE 5.13: HOMO SAPIENS: SUMMARY STATISTICS: FACE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F14	M	10	2.4990	0.189	0.060	1.03	0.964	2.29	18	0.034
	F	10	2.3070	0.186	0.059					
F15	M	10	0.9610	0.159	0.050	1.40	0.625	1.35	18	0.194
	F	10	0.8560	0.188	0.059					
F16	M	9	0.7900	0.184	0.061	1.33	0.680	2.60	17	0.019
	F	10	0.5850	0.160	0.050					
F17	M	10	9.0790	0.349	0.110	2.15	0.269	2.47	18	0.024
	F	10	8.5950	0.512	0.162					
F18	M	9	4.7789	0.178	0.059	3.63	0.097	2.30	14	0.037
	F	7	4.4771	0.340	0.128					
F19	M	9	5.5900	0.259	0.086	2.19	0.295	4.03	15	0.001
	F	8	4.9587	0.382	0.135					
F20	M	9	3.6556	0.405	0.135	1.26	0.770	3.20	15	0.006
	F	8	3.0575	0.360	0.127					
F21	M	10	2.3010	0.198	0.062	1.29	0.711	1.39	18	0.183
	F	10	2.1700	0.224	0.071					
F22	M	10	9.6200	0.667	0.211	2.64	0.165	2.72	18	0.014
	F	10	8.9460	0.410	0.130					
F23	M	10	7.6960	0.315	0.100	1.03	0.970	3.36	18	0.003
	F	10	7.2190	0.319	0.101					
F24	M	10	10.3300	0.410	0.130	1.17	0.816	4.44	18	0.000
	F	10	9.5450	0.379	0.120					
F25	M	10	9.5000	0.688	0.218	2.14	0.272	2.45	18	0.025
	F	10	8.8550	0.470	0.149					
F26	M	9	1.0622	0.308	0.103	1.12	0.892	1.15	15	0.269
	F	8	0.8950	0.290	0.103					
F27	M	9	0.4533	0.073	0.024	1.75	0.473	1.77	15	0.098
	F	8	0.3975	0.055	0.019					

* value for males and females

TABLE 5.14: HOMINOIDS: COEFFICIENT OF VARIATION: FACE

SP	SEX	F1	F2	F3	F4	F5	F6	
HS		4.59	8.61	6.17	4.09	39.58	5.47	
HS	M	3.66	10.10	5.29	4.07	24.34	3.29	
HS	F	4.27	7.12	6.64	3.98	44.53	4.15	
PA		5.41	20.12	5.84	7.10	24.97	6.36	
PA	M	2.95	13.85	5.19	6.43	18.24	3.81	
PA	F	5.90	24.57	4.93	7.66	26.93	7.49	
GO		9.29	23.31	7.88	8.28	24.66	10.06	
GO	M	5.08	15.17	7.13	8.21	10.91	3.53	
GO	F	3.87	14.66	3.30	6.97	15.39	3.28	
PO		9.11	26.48	9.58	6.59	43.13	11.35	
PO	M	6.64	23.59	9.24	6.11	49.76	9.59	
PO	F	4.24	15.45	5.05	4.92	31.93	6.11	
SP	SEX	F7	F8	F9	F10	F11	F12	F13
HS		6.96	4.47	5.69	11.62	6.49	7.72	7.19
HS	M	4.64	3.77	3.51	12.96	6.25	6.66	5.78
HS	F	6.50	3.69	7.13	10.26	6.62	6.21	6.47
PA		5.93	5.64	5.94	12.58	7.18	11.21	12.12
PA	M	5.33	4.32	6.41	12.98	6.74	6.10	7.26
PA	F	3.65	4.66	3.39	11.49	5.63	14.39	14.68
GO		12.65	10.90	10.24	16.38	12.94	12.48	15.17
GO	M	4.54	6.92	6.71	10.30	8.03	11.83	15.25
GO	F	3.48	3.04	5.35	9.50	6.54	3.29	3.46
PO		13.65	11.24	11.51	17.62	12.05	16.92	14.57
PO	M	11.46	8.68	10.88	13.10	9.06	13.01	10.60
PO	F	7.82	6.07	5.67	12.35	6.83	11.39	10.60

TABLE 5.14: HOMINOIDS: COEFFICIENT OF VARIATION: FACE:CONT'D

SP	SEX	F14	F15	F16	F17	F18	F19	F20
HS		8.62	19.54	28.87	5.59	6.35	8.51	14.33
HS	M	7.55	16.51	23.25	3.85	3.73	4.63	11.09
HS	F	8.05	21.93	27.27	5.96	7.59	7.71	11.79
PA		9.04	43.76	17.41	5.25	7.37	6.55	12.97
PA	M	8.21	33.87	21.42	5.40	8.05	6.67	13.94
PA	F	8.65	56.51	13.47	4.31	6.61	6.26	12.69
GO		10.60	39.52	37.67	9.79	12.35	13.71	21.05
GO	M	10.21	29.12	35.64	6.72	10.80	10.34	6.67
GO	F	7.52	50.32	16.82	4.82	4.28	8.77	8.72
PO		13.36	63.79	22.83	9.61	13.24	15.08	22.66
PO	M	8.12	56.28	26.66	8.46	10.36	11.92	19.05
PO	F	13.51	56.12	19.75	5.80	9.18	10.41	12.40

SP	SEX	F21	F22	F23	F24	F25	F26	F27
HS		9.68	6.90	5.28	5.60	7.22	30.76	16.22
HS	M	8.58	6.93	4.09	3.97	7.25	28.95	16.06
HS	F	10.33	4.59	4.42	3.97	5.31	32.43	13.83
PA		10.84	6.46	5.91	5.60	6.19	18.33	33.96
PA	M	12.49	4.68	5.51	4.74	4.25	16.01	31.08
PA	F	9.21	7.41	4.82	6.26	7.14	15.42	25.37
GO		16.95	13.49	11.97	10.75	14.34	16.47	29.67
GO	M	7.78	8.21	10.58	5.74	8.89	14.24	18.49
GO	F	9.33	4.82	3.06	6.40	5.08	10.41	22.06
PO		22.10	12.58	9.13	8.28	12.05	22.77	38.05
PO	M	15.50	8.78	7.15	9.02	8.68	16.27	29.41
PO	F	14.47	4.32	6.59	3.97	5.11	18.82	20.30

Sex differences in mean values

There was a significant difference between the sexes in the means of 17 variables at the 5 % level or less (F1, F5 - 8, F12 - 14, F16 - 20, F22 - 25) (see table 5.13) and percentage sexual dimorphism in the face ranges from 61.7 (F5) to 102.4 (F4) % (see table 5.15). F5 (glabella projection) is a small measurement so the difference between the means of the sexes has been magnified but the ranges of male and female values for F4 (orbital height) greatly overlap. The mean percentage sexual dimorphism is 90.9 per cent. The majority of measurements where there was a significant difference between the means of males and females are ones of width which corresponds to the analysis of the mandible and palate. The rest are mostly related to differences in the degree of prognathism (or facial prominence) which fits in with the analysis of the base.

5.3.6 Overall Effect On Cranium

For *H. sapiens* the major discriminants of males and females are size (width of palate, mandible, base, and face) and facial projection. The areas of size difference are functionally correlated such that the size of one effects all of the others. For example, the wider the mandible, the wider the palate, base, and face.

The cheekbones of the male specimens were more prominent, on average, than those of the females. This may correlate with the basicranial angle, where a larger angle results in a more prominent face. Another area of difference between the sexes is the nuchal region which is more variable in males than in females. In most traits, however, females are more variable than males.

The mandible is the most dimorphic region for *H. sapiens* (mean percentage sexual dimorphism of 88.7 per cent) and the vault the least (95.2 %) but overall *H. sapiens* is not very variable or dimorphic in the traits measured.

5.4 Pan

5.4.1 Mandible

Sex differences in variance

There is a statistically significant differences between the sexes in variance for M4 (Minimum ramus breadth), M8 (Maximum internal breadth), and M9 (Maximum external breadth) at the 5 % level (see table 5.16). The values of CV for the species range from 5.37 (M9) to 12.28 (M5) (see table 5.02). The values for males range from 3.32 (M9) to 13.44 (M7), males are more variable than females in four variables

TABLE 5.15: HOMINOIDS: PERCENTAGE SEXUAL DIMORPHISM: FACE

	F1	F2	F3	F4	F5	F6	F7	F8	F9
HS	89.3	97.9	96.1	102.4	61.7	92.3	92.3	95.1	96.7
PA	94.2	86.6	94.1	96.5	78.0	94.6	93.1	93.3	94.2
GO	85.3	70.2	89.7	93.2	65.6	83.1	79.1	83.2	85.1
PO	86.9	72.5	89.0	93.0	84.4	85.6	83.2	84.9	86.5

	F10	F11	F12	F13	F14	F15	F16	F17	F18
HS	96.0	96.7	91.6	92.4	92.3	89.1	74.1	94.7	93.7
PA	92.9	92.8	92.5	90.3	92.8	91.4	100.3	95.8	96.9
GO	77.3	81.1	84.6	82.8	89.3	75.9	65.5	85.8	84.0
PO	78.5	83.9	79.4	81.8	85.0	55.7	100.1	88.4	83.8

	F19	F20	F21	F22	F23	F24	F25	F26	F27	MEAN
HS	88.7	83.6	94.3	93.0	93.8	92.4	93.2	84.3	87.6	90.9
PA	96.6	100.1	97.0	95.3	94.2	97.0	95.2	121.7	70.5	94.0
GO	82.4	67.7	74.8	79.7	84.2	83.9	78.7	81.2	64.2	79.9
PO	81.9	74.1	72.6	81.7	88.7	91.7	82.9	74.2	59.1	81.8

TABLE 5.16: PAN: SUMMARY STATISTICS: MANDIBLE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
M1	M	10	8.8960	0.668	0.211	1.81	0.389	2.31	18	0.033
	F	10	8.0780	0.899	0.284					
M2	M	10	4.3450	0.281	0.089	1.69	0.449	-0.21	18	0.834
	F	10	4.3760	0.364	0.115					
M3	M	10	12.4300	0.591	0.187	2.01	0.313	2.50	18	0.022
	F	10	11.6200	0.838	0.265					
M4	M	10	4.5750	0.421	0.133	4.23	0.043	3.55	18	0.002
	F	10	4.0490	0.205	0.065					
M5	M	10	3.4490	0.339	0.107	1.14	0.845	2.56	18	0.020
	F	10	3.0470	0.362	0.115					
M6	M	10	6.4250	0.384	0.121	1.60	0.494	3.61	18	0.002
	F	10	5.8660	0.304	0.096					
M7	M	10	1.6420	0.221	0.070	1.42	0.607	-0.19	18	0.854
	F	10	1.6590	0.185	0.058					
M8	M	10	4.0650	0.181	0.057	4.48	0.036	1.18	18	0.254
	F	10	3.9070	0.383	0.121					
M9	M	10	5.4860	0.182	0.058	4.35	0.039	0.60	18	0.555
	F	10	5.4060	0.379	0.120					
M10	M	10	2.7550	0.220	0.070	1.16	0.827	2.00	18	0.060
	F	10	2.5500	0.237	0.075					
M11	M	10	2.7360	0.223	0.071	1.05	0.946	1.81	18	0.087
	F	10	2.5530	0.228	0.072					
M12	M	10	6.5600	0.423	0.134	1.05	0.949	0.37	18	0.713
	F	10	6.4900	0.414	0.131					
	*	value	for	males	and	females				

(M4, M6, M7, M12), and are more variable than the species in two cases (M7, M12). Female values range from 5.06 (M4) to 11.89 (M5) and females are more variable than the species in seven cases (M1, M2, M3, M8, M9, M10, M12). Both males and females are more variable than the species for M12 (arcadal length). Thus the difference in variance between the sexes occurs in two width measurements (M8 and M9) and the breadth of the ramus (M4).

Sex differences in mean values

There was a significant difference between the means of the sexes in five cases (M1, M3 to 6) at the 5 % level or less (see table 5.16) and percentage sexual dimorphism for the mandible ranges from 88.3 (M5) to 101.0 (M7) % (see table 5.03). For M5 (symphyseal height) the ranges overlap but males are more variable than females. For M7 (thickness of the mandibular corpus) there is a large overlap in the ranges of the values for males and females but one small value for one male acts to reduce the male mean making it smaller than the female mean. The mean value for percentage sexual dimorphism is 94.5 % which is actually less than the value for *H. sapiens.* The difference between the means of the sexes occurs in variables which are associated with length, breadth, and height of the mandible and thus are most probably related to size differences between the sexes.

5.4.2 Palate

Sex differences in variance

There was no significant difference between the variances of the sexes for any variable at the 5 % level or less (see table 5.17). The values of CV for the species range from 5.31 (P6) to 14.93 (P8) (see table 5.05) where P7 and P8 are variable for the same reasons as in *H. sapiens.* Male values range from 4.04 (P6) to 13.04 (P7), males are more variable than females in 3 cases (P1, P5, P7), and are more variable than the species in 2 cases (P5, P7). Female values range from 4.58 (P5) to 16.06 (P8) and females are more variable than the species in 6 cases (P2, P3, P4, P6, P8, P9). Thus females have higher values of CV than males in the majority of characters even though neither sex is very variable in palatal measurements of variance.

Sex differences in mean values

There is no significant difference between the means of the sexes in any palatal character (see table 5.17). Percentage sexual dimorphism for the palate has a range of 89.1 (P8) to 101.0 (P4) % (see table 5.06) where for P8 (depth at M3) the ranges overlap but males are more variable than females and for P4 (external breadth) fe-

TABLE 5.17: PAN: SUMMARY STATISTICS: PALATE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
P1	M	10	6.7750	0.553	0.175	1.24	0.755	2.07	18	0.053
	F	10	6.2880	0.497	0.157					
P2	M	10	3.6370	0.175	0.055	3.40	0.083	-0.09	18	0.932
	F	10	3.6470	0.322	0.102					
P3	M	10	7.1910	0.373	0.118	2.39	0.211	1.26	18	0.223
	F	10	6.9170	0.576	0.182					
P4	M	10	5.9080	0.242	0.076	3.07	0.110	-0.37	18	0.716
	F	10	5.9650	0.424	0.134					
P5	M	9	6.8711	0.533	0.178	2.93	0.149	0.36	16	0.726
	F	9	6.7978	0.311	0.104					
P6	M	10	5.8130	0.235	0.074	2.64	0.164	-0.02	18	0.983
	F	10	5.8160	0.382	0.121					
P7	M	10	1.2640	0.165	0.052	2.37	0.216	1.29	18	0.215
	F	10	1.1840	0.107	0.034					
P8	M	10	1.3540	0.166	0.052	1.37	0.648	1.84	18	0.083
	F	10	1.2060	0.194	0.061					
P9	M	10	3.5050	0.274	0.087	1.49	0.563	-0.45	18	0.655
	F	10	3.5670	0.334	0.106					

* value for males and females

males have a wider range of values which totally overlap the male range of values. The mean value of percentage sexual dimorphism is 97.1 %. Thus the palate is not a dimorphic region of the cranium in *Pan.*

5.4.3 Base

Sex differences in variance

The variances of the sexes for 4 variables are significantly different at the 5 % level or less (B18, B21, B22, B23) (see table 5.18) where B18 (bimastoid breadth) is a width measurement and B21 and B22 are related to the kyphosis of the cranium.

The values of CV for the species range from 5.18 (B14) to 63.37 (B23) (see table 5.08). B23 and B24 are highly variable for the species, males, and females due to the reasons given for *H. sapiens* above. B20 (Lateral nuchal crest arc) is highly variable (CV=19.21), due to variation in nuchal crest development and B19 (Nuchal crest width) is variable for females (CV=16.68) but not males (CV=11.79). Male values range from 3.51 (B9) to 67.75 (B23) and males are more variable than females in 8 cases (B6, B7, B11, B12, B13, B16, B20, B23) in which they are also more variable than the species except for B7 (bipetrous width) where the CV for the species is approximately equal to that for males. Female values range from 4.73 (B17) to 42.69 (B23) and females are more variable than the species in 12 cases (B1, B2, B5, B8, B9, B14, B15, B18, B19, B21, B22, B23). Thus females have higher values of CV than males for more characters in this region of the skull.

Sex differences in mean values

There was a significant difference between the means of the sexes in four cases (B3, B10, B15, B17) at the 5 % level or less (see table 5.18) where B3, B10, and B17 are width measurements of the base and B15 is related to kyphosis of the base. Differences between the sexes in both variances and means arise in these areas which ties in with the sex differences which occurred in the mandible.

Percentage sexual dimorphism for the base has a range of 68.2 (B23) to 100.7 (B21) % (see table 5.09). B23 (articular eminence height) is a small measurement so although the ranges of male and female values overlap the difference in means is accentuated but for B21 (sphenooccipital synchrondosis-staphlyon chord) females are more variable than males with a larger range of values making the mean value slightly higher than the male value. The mean value of percentage sexual dimorphism is 94.2 %.

TABLE 5.18: PAN: SUMMARY STATISTICS: BASE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B1	M	10	2.8380	0.294	0.093	1.15	0.834	1.00	18	0.333
	F	10	2.7020	0.316	0.100					
B2	M	10	2.4370	0.165	0.052	2.81	0.140	0.66	18	0.518
	F	10	2.3700	0.276	0.087					
B3	M	10	10.3290	0.534	0.169	1.44	0.593	2.47	18	0.024
	F	10	9.6770	0.641	0.203					
B4	M	10	6.4070	0.335	0.106	1.08	0.910	2.04	18	0.056
	F	10	6.1070	0.323	0.102					
B5	M	10	5.8580	0.306	0.097	1.46	0.584	1.43	18	0.170
	F	10	5.6410	0.369	0.117					
B6	M	10	4.2900	0.281	0.089	1.53	0.538	1.81	18	0.087
	F	10	4.0830	0.228	0.072					
B7	M	10	2.4370	0.164	0.052	1.16	0.825	1.27	18	0.219
	F	10	2.3470	0.152	0.048					
B8	M	10	4.2660	0.206	0.065	2.80	0.141	-0.09	18	0.926
	F	10	4.2780	0.345	0.109					
B9	M	10	5.0320	0.177	0.056	3.93	0.054	0.10	18	0.924
	F	10	5.0200	0.350	0.111					
B10	M	10	3.1940	0.329	0.104	1.02	0.982	2.54	18	0.021
	F	10	2.8220	0.327	0.103					
B11	M	10	2.4320	0.208	0.066	1.86	0.369	1.47	18	0.159
	F	10	2.3120	0.153	0.048					
B12	M	10	4.9290	0.518	0.164	2.78	0.144	1.15	18	0.267
	F	10	4.7100	0.311	0.098					

* value for males and females

TABLE 5.18: PAN: SUMMARY STATISTICS: BASE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B13	M	10	2.5980	0.366	0.116	2.62	0.167	1.69	18	0.108
	F	10	2.3680	0.226	0.071					
B14	M	10	5.2800	0.230	0.073	1.65	0.466	1.31	18	0.207
	F	10	5.1250	0.296	0.093					
B15	M	10	2.6960	0.213	0.067	2.49	0.191	2.23	18	0.039
	F	10	2.4160	0.336	0.106					
B16	M	10	8.3790	0.789	0.249	3.07	0.110	0.91	18	0.377
	F	10	8.1190	0.450	0.142					
B17	M	10	12.1910	0.537	0.170	1.01	0.989	3.29	18	0.004
	F	10	11.4000	0.539	0.170					
B18	M	10	8.3690	0.413	0.131	4.99	0.025	1.17	18	0.259
	F	10	7.9960	0.923	0.292					
B19	M	10	5.5680	0.657	0.208	1.60	0.493	1.75	18	0.097
	F	10	4.9820	0.831	0.263					
B20	M	10	7.3900	1.677	0.530	2.08	0.289	0.22	18	0.831
	F	10	7.2500	1.162	0.367					
B21	M	10	3.5430	0.212	0.067	5.77	0.015	-0.15	18	0.883
	F	10	3.5690	0.509	0.161					
B22	M	10	5.9330	0.226	0.071	5.85	0.015	1.07	18	0.299
	F	10	5.7330	0.547	0.173					
B23	M	10	0.3590	0.243	0.077	5.41	0.019	1.36	18	0.190
	F	10	0.2450	0.105	0.033					
B24	M	10	0.5350	0.102	0.032	1.88	0.362	0.42	18	0.679
	F	10	0.5120	0.140	0.044					

* value for males and females

5.4.4 Vault

Sex differences in variance

The variance of the sexes was significantly different in none of the characters (see table 5.19). The values of CV for the species range from 4.12 (V9) to 36.39 (V24) (see table 5.11). V23 and V24 (mastoid length and width) were difficult to measure in the Frankfurt horizontal plane and this may have contributed to the variability of these measurements. V11 to 14 (lambda - inion, inion - opisthion, chord and arc measurements) are possibly variable due to the fact that the position of inion (located on the inferior nuchal line) depends on the size of the nuchal muscles which in turn depends on factors such as jaw size and the needs of the masticatory system as well as balance. Thus inion will be positioned high up on the occipital bone if the nuchal muscles are large. Male values range from 3.58 (V9) to 31.53 (V24), males are more variable than females in 9 cases (V1, V4, V7, V8, V10, V13, V14, V19, V20), and are more variable than the species in 7 of these cases (all but V4 and V19). Female values range from 3.71 (V11) to 41.28 (V24) and are more variable than the species in 11 cases (V2, V5, V6, V9, V11, V12, V17, V21 - 24). Thus females have higher values of CV in more characters than do males and sex differences in variance, apart from the cases described above, occurs primarily in the nuchal muscle attachment area.

Sex differences in mean values

There are 8 cases where the means of the sexes are significantly different at the 5 % level (V3, V4, V15, V16, V17, V19, V20, V22) (see table 5.19). Variability in the vault occurs in width measurements (V17 and V22) which accords with the analysis of the base. V19 and V20 are related to the position of the malar region and are probably correlated strongly with V15 and V16, temporal muscle measurements while V3 and V4 are frontal bone measurements and may vary due to the extent of glabella projection.

The percentage sexual dimorphism for the vault ranges from 82.3 (V24) to 105.8 (V11) % (see table 5.12). V24 (mastoid width) is a variable character for both males and females and there is a large overlap of ranges. V11 (inion chord) is a variable character for both males and females which may be related to the nuchal crest; the stronger the crest, the higher inion is located and the less the distance from lambda to inion, which would account for the male mean being less than the female mean. The mean value of percentage sexual dimorphism for the vault is 95.2 %.

TABLE 5.19: PAN: SUMMARY STATISTICS: VAULT

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V1	M	10	8.2860	0.408	0.129	1.78	0.406	0.15	18	0.879
	F	10	8.2610	0.306	0.097					
V2	M	10	9.7400	0.398	0.126	1.17	0.815	0.64	18	0.529
	F	10	9.6210	0.431	0.136					
V3	M	10	8.2400	0.450	0.142	1.04	0.958	2.20	18	0.041
	F	10	7.8000	0.442	0.140					
V4	M	10	7.2980	0.383	0.121	1.17	0.819	2.14	18	0.046
	F	10	6.9450	0.354	0.112					
V5	M	10	6.6850	0.456	0.144	2.95	0.123	-0.12	18	0.904
	F	10	6.7200	0.783	0.248					
V6	M	10	6.3130	0.447	0.141	2.33	0.223	0.03	18	0.979
	F	10	6.3060	0.682	0.216					
V7	M	10	6.3000	0.655	0.207	1.80	0.396	0.74	18	0.472
	F	10	6.1100	0.489	0.155					
V8	M	10	5.2240	0.511	0.161	2.69	0.156	0.33	18	0.747
	F	10	5.1620	0.311	0.098					
V9	M	10	8.8050	0.315	0.100	1.58	0.509	1.10	18	0.288
	F	10	8.6300	0.395	0.125					
V10	M	10	5.1560	0.483	0.153	2.58	0.174	1.07	18	0.298
	F	10	4.9630	0.301	0.095					
V11	M	9	2.0778	0.495	0.165	1.36	0.678	-0.49	17	0.631
	F	10	2.1990	0.577	0.182					
V12	M	9	2.2889	0.523	0.174	1.33	0.702	0.11	17	0.913
	F	10	2.2600	0.602	0.190					

* value for males and females

TABLE 5.19: PAN: SUMMARY STATISTICS: VAULT CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V13	M	10	3.8630	0.729	0.231	2.11	0.281	0.86	18	0.401
	F	10	3.6220	0.502	0.159					
V14	M	10	4.1800	0.796	0.252	2.39	0.210	1.27	18	0.221
	F	10	3.8000	0.514	0.163					
V15	M	10	7.6810	0.678	0.215	1.16	0.829	2.32	18	0.032
	F	10	6.9480	0.731	0.231					
V16	M	10	23.9600	2.211	0.699	1.27	0.728	2.88	18	0.010
	F	10	20.9260	2.491	0.788					
V17	M	10	10.5730	0.480	0.152	1.76	0.411	2.40	18	0.027
	F	10	9.9680	0.637	0.201					
V18	M	10	8.7220	0.428	0.135	1.07	0.924	1.71	18	0.105
	F	10	8.4000	0.415	0.131					
V19	M	10	8.4850	0.453	0.143	1.48	0.567	2.22	18	0.039
	F	10	8.0730	0.372	0.118					
V20	M	10	7.8110	0.472	0.149	1.62	0.485	2.99	18	0.008
	F	10	7.2430	0.371	0.117					
V21	M	10	13.1250	0.527	0.167	1.26	0.733	1.89	18	0.074
	F	10	12.6500	0.593	0.187					
V22	M	10	11.3690	0.438	0.139	1.10	0.892	2.50	18	0.022
	F	10	10.8660	0.459	0.145					
V23	M	10	1.8860	0.433	0.137	2.13	0.276	1.09	18	0.292
	F	10	1.6230	0.631	0.200					
V24	M	10	1.9770	0.623	0.197	1.16	0.828	1.21	18	0.243
	F	10	1.6270	0.672	0.212					

* value for males and females

5.4.5 Face

Sex differences in variance

There is a statistically significant difference between the variances of the sexes (p=.05) in 2 cases (F9, F12) (see table 5.20). F9 (bimaxillary chord) is a width measurement and correlates with the variation in measurements V19 and V20 (see vault section) whereas F12 is a measure of facial height and the variation in this measurement may be influenced by the degree of kyphosis, that is, the smaller the basicranial angle, the shorter the face.

The species values of CV have a range of 5.25 (F17) to 43.76 (F15) (see table 5.14). F15 (simotic chord) was very difficult to measure in the Pongids since the nasal suture fuses early in life and so the accuracy of this measurement is doubtful. F2 (interorbital breadth) (CV=20.12) is more variable for females and F5 (glabella projection) (CV=24.97) is variable for both males and females. F16, F26, and F27 are variable due to the reasons given above for *H. sapiens.* Male values range from 2.95 (F1) to 33.87 (F15) with males being more variable than females in 14 cases (F3, F7, F9 - 11, F16 - 21, F23, F26, F27), and more variable than the species in 8 cases (F9, F10, F16 - 21). Female values range from 3.39 (F9) to 56.51 (F15) and females are more variable than the species in 11 cases (F1, F2, F4 - 6, F12, F13, F15, F22, F24, F25). Thus males have higher values of CV in more characters than do females.

Sex differences in mean values

The means of the sexes were significantly different (p=.05 or less) in 11 cases (F1, F3, F5 - 9, F11, F23, F26, F27) (see table 5.20). The difference between the means for F23 (lateral facial length) accords with the measurements V19 and V20 while the variability of the glabella projection (F5) accounts for the variability in frontal bone measurements. The remaining measurements of the face which show a significant difference between the means of the sexes are ones of breadth. The difference in size in the malar region could be affected by the size of the masticatory muscles but width measurements in the orbital region may be affected by the pull of the temporal muscle as well as the size of the masticatory muscles and their effect on the lower face.

Percentage sexual dimorphism for the face has a range of 78.0 (F5) to 121.7 (F26) % (see table 5.15). F5 is a small measurement and thus the differences in the means of male and female values is magnified. F26 is also a small measurement which is variable for males and females. The mean value of percentage sexual dimorphism for the face is 94 %.

TABLE 5.20: PAN: SUMMARY STATISTICS: FACE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F1	M	10	8.8940	0.262	0.083	3.55	0.073	2.92	18	0.009
	F	10	8.3780	0.494	0.156					
F2	M	10	2.1200	0.294	0.093	2.36	0.217	1.67	18	0.112
	F	10	1.8360	0.451	0.143					
F3	M	10	3.5130	0.182	0.058	1.25	0.747	2.69	18	0.015
	F	10	3.3050	0.163	0.052					
F4	M	10	3.3910	0.218	0.069	1.32	0.682	1.12	18	0.276
	F	10	3.2730	0.251	0.079					
F5	M	10	1.1320	0.206	0.065	1.33	0.681	2.50	18	0.022
	F	10	0.8830	0.238	0.075					
F6	M	10	10.6340	0.406	0.128	3.45	0.079	2.11	18	0.049
	F	10	10.0630	0.754	0.238					
F7	M	10	12.5460	0.669	0.212	2.48	0.193	3.62	18	0.002
	F	10	11.6380	0.425	0.134					
F8	M	10	9.5810	0.414	0.131	1.01	0.985	3.47	18	0.003
	F	10	8.9370	0.416	0.132					
F9	M	10	9.1350	0.586	0.185	4.04	0.049	2.57	18	0.019
	F	10	8.6030	0.291	0.092					
F10	M	10	3.0990	0.402	0.127	1.48	0.569	1.34	18	0.196
	F	10	2.8780	0.331	0.105					
F11	M	10	5.5750	0.376	0.119	1.66	0.461	2.65	18	0.016
	F	10	5.1760	0.292	0.092					
F12	M	10	8.4910	0.518	0.164	4.77	0.029	1.61	18	0.124
	F	10	7.8560	1.131	0.358					
F13	M	10	6.1260	0.445	0.141	3.33	0.088	2.04	18	0.057
	F	10	5.5300	0.812	0.257					

* value for males and females

TABLE 5.20: PAN: SUMMARY STATISTICS: FACE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F14	M	10	2.7750	0.228	0.072	1.05	0.948	1.97	18	0.064
	F	10	2.5760	0.223	0.070					
F15	M	6	0.7217	0.244	0.100	2.33	0.375	0.34	10	0.742
	F	6	0.6600	0.373	0.152					
F16	M	10	0.8120	0.174	0.055	2.52	0.185	-0.03	18	0.976
	F	10	0.8140	0.110	0.035					
F17	M	10	8.6790	0.469	0.148	1.71	0.435	1.93	18	0.069
	F	10	8.3180	0.358	0.113					
F18	M	10	4.9990	0.403	0.127	1.58	0.506	0.95	18	0.356
	F	10	4.8450	0.320	0.101					
F19	M	10	5.6270	0.375	0.119	1.21	0.779	1.19	18	0.251
	F	10	5.4370	0.341	0.108					
F20	M	10	3.8510	0.537	0.170	1.20	0.787	-0.02	18	0.983
	F	10	3.8560	0.489	0.155					
F21	M	10	2.8010	0.350	0.111	1.96	0.332	0.62	18	0.545
	F	10	2.7170	0.250	0.079					
F22	M	10	13.1610	0.616	0.195	2.28	0.235	1.75	18	0.098
	F	10	12.5450	0.930	0.294					
F23	M	10	7.3820	0.407	0.129	1.47	0.575	2.56	18	0.020
	F	10	6.9550	0.336	0.106					
F24	M	10	9.7550	0.462	0.146	1.64	0.470	1.22	18	0.238
	F	10	9.4650	0.593	0.187					
F25	M	10	13.1420	0.559	0.177	2.56	0.178	1.89	18	0.075
	F	10	12.5130	0.893	0.283					
F26	M	10	0.6850	0.110	0.035	1.37	0.643	-2.79	18	0.012
	F	10	0.8340	0.129	0.041					
F27	M	10	0.3660	0.114	0.036	3.02	0.115	2.60	18	0.018
	F	10	0.2580	0.065	0.021					

* value for males and females

5.4.6 Overall Effect On Cranium

The width of the mandible affects the width of the cranial base and the angle of the basicranium affects facial projection. A large, wide mandible would mean a wide cranial base, larger chewing muscles for efficient mastication, wider zygomatic/ malar region which may affect the width of the orbital area. The heavier the mandible, the more strength in the nuchal muscle area is needed to balance the skull, thus affecting measurements in this area. This correlation of functions probably causes the variation seen in the various regions of the skull of *Pan*.

On the basis of the univariate study of *Pan*, the main cause of difference between the sexes is size; size differences which result in some differences in shape. Shape differences are most notable in the nuchal muscle attachment area. Also, a difference between sexes in the size of the temporal muscle may be the cause of the difference in malar projection (more room needed for a larger muscle) and the subsequent effects on the face. *Pan* is not very dimorphic in any region with the mean percentage sexual dimorphism ranging from 94% in the base to 97% in the palate. *Pan* has the same mean value of percentage dimorphism in the vault region as *H. sapiens* but in all other regions is less dimorphic overall.

5.5 Gorilla

5.5.1 Mandible

Sex differences in variance

The variances of the sexes are significantly different in 1 case (M4 -minimum ramus breadth) at the 5 % level (see table 5.21) and the values of CV for the species range from 4.18 (M9) to 17.43 (M5) (see table 5.02). The values of CV for M4, M5 (symphyseal height), and M6 (coronoid height) are high for the species but not for males and females when considered separately, probably due to differences in size of the two sexes. Male values range from 2.51 (M9) to 12.74 (M5) with males being more variable than females in seven cases (M3 - M8, M12), and more variable than the species in one case (M8). Female values range from 3.93 (M12) to 10.3 (M8) and females are more variable than the species in one case (M9 -external breadth).

Sex differences in mean values

In eleven cases (all but M8 -internal breadth) there is a significant difference between the means of male and female values at the 5 % level or less (see table 5.21). Percentage sexual dimorphism has a range of 73.7 (M4) to 96.0 (M9) % (see table 5.03). For M4 (ramus breadth) the ranges of male and female values just overlap but

TABLE 5.21: GORILLA: SUMMARY STATISTICS: MANDIBLE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
M1	M	10	11.5450	1.007	0.318	1.30	0.706	5.19	18	0.000
	F	10	9.3450	0.884	0.280					
M2	M	10	4.9040	0.221	0.070	1.27	0.729	4.08	18	0.001
	F	10	4.4740	0.249	0.079					
M3	M	10	16.5050	1.091	0.345	2.03	0.305	6.82	18	0.000
	F	10	13.6300	0.765	0.242					
M4	M	10	7.1980	0.594	0.188	4.16	0.045	9.05	18	0.000
	F	10	5.3060	0.291	0.092					
M5	M	10	5.0890	0.648	0.205	3.94	0.053	5.14	18	0.000
	F	10	3.9100	0.326	0.103					
M6	M	10	12.0500	0.952	0.301	1.91	0.348	7.56	18	0.000
	F	10	9.2410	0.688	0.218					
M7	M	10	2.5520	0.214	0.068	1.43	0.600	2.80	18	0.012
	F	10	2.3050	0.179	0.056					
M8	M	10	4.6000	0.543	0.172	1.45	0.592	0.96	18	0.349
	F	10	4.3850	0.452	0.143					
M9	M	10	6.7140	0.168	0.053	3.24	0.095	2.45	18	0.025
	F	10	6.4460	0.303	0.096					
M10	M	10	4.1050	0.217	0.068	1.86	0.368	5.21	18	0.000
	F	10	3.5010	0.296	0.093					
M11	M	10	4.1900	0.270	0.085	1.51	0.546	5.61	18	0.000
	F	10	3.4300	0.332	0.105					
M12	M	10	9.6330	0.601	0.190	3.36	0.086	5.97	18	0.000
	F	10	8.3400	0.328	0.104					
	*	value	for	males	and	females				

males are more variable than females. For M9 (external breadth) the female range totally overlaps the male range with female values being more variable than male values. The mean percentage sexual dimorphism for the mandible is 84.8 %. Thus the main cause of difference between male and female *Gorilla* mandibles is probably size.

5.5.2 Palate

Sex differences in variance

There was no significant difference between the variances of males and females for any variable at the 5 % level or less (see table 5.22). The values of CV for the species range from 6.7 (P6) to 18.22 (P7) (see table 5.05). P7 (depth at M1) and, to a certain extent P8 (depth at M3) values for CV are affected by the high values for females. Male values range from 3.74 (P6) to 14.03 (P7), males are more variable than females in four cases (P1, P3, P5, P9 - length measurements), and are more variable than the species in one case (P9 -bicanine breadth). Female values range from 4.01 (P5) to 20.67 (P7) and are more variable than the species in two cases (P7, P8). Thus, apart from P7 and P8, the sexes are not very variable in palatal measurements.

Sex differences in mean values

There was a significant difference between the means of male and female values in 6 cases (P1 - P6) at the 1 % level (see table 5.22). Percentage sexual dimorphism has a range of 81.0 (P1) to 91.0 (P4) % (see table 5.06). For P1 (palate length) the ranges of males and females overlap because females are variable for this character whereas for P4 (external breadth) there is a considerable overlap in the ranges of males and females. The mean value of percentage sexual dimorphism for the palate is 87.7 %. A significant sexual difference occurs between the means of length and width measurements and thus the main source of difference between the sexes would seem to be size.

5.5.3 Base

Sex differences in variance

There was no significant difference between the variances of males and females for any character at the 5 % level or less (see table 5.23). The values of CV for the species range from 7.02 (B9) to 50.47 (B23) (see table 5.08) B23 and B24 are highly variable due to the reasons given above for *H. sapiens* and B20 for the reasons given above for *Pan*. In seven cases (B10, B12 - 14, B16, B21, B22) the large values of

TABLE 5.22: GORILLA: SUMMARY STATISTICS: PALATE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
P1	M	10	10.4140	0.981	0.310	3.26	0.093	5.59	18	0.000
	F	10	8.4310	0.543	0.172					
P2	M	9	4.2400	0.286	0.095	1.11	0.869	3.67	17	0.002
	F	10	3.7700	0.271	0.086					
P3	M	10	10.8380	0.793	0.251	3.52	0.075	6.58	18	0.000
	F	10	8.9690	0.423	0.134					
P4	M	10	7.4110	0.281	0.089	1.93	0.341	4.40	18	0.000
	F	10	6.7410	0.391	0.124					
P5	M	8	10.2650	0.663	0.234	3.57	0.080	6.24	16	0.000
	F	10	8.7510	0.351	0.111					
P6	M	9	7.2800	0.272	0.091	1.68	0.479	4.58	16	0.000
	F	9	6.5989	0.353	0.118					
P7	M	10	1.8680	0.262	0.083	1.65	0.470	1.79	18	0.091
	F	10	1.6270	0.336	0.106					
P8	M	10	1.9220	0.205	0.065	1.92	0.346	1.47	18	0.159
	F	10	1.7590	0.284	0.090					
P9	M	10	4.2310	0.588	0.186	1.97	0.327	1.74	18	0.099
	F	10	3.8340	0.419	0.133					
	*	value	for	males	and	females				

TABLE 5.23: GORILLA: SUMMARY STATISTICS: BASE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B1	M	9	3.3967	0.211	0.070	1.33	0.674	3.19	17	0.005
	F	10	3.1090	0.183	0.058					
B2	M	9	3.0989	0.152	0.051	2.55	0.202	4.55	17	0.000
	F	10	2.6710	0.242	0.077					
B3	M	10	14.1640	0.759	0.240	2.42	0.205	8.00	18	0.000
	F	10	11.8820	0.488	0.154					
B4	M	10	8.5080	0.554	0.175	2.51	0.187	4.19	18	0.001
	F	10	7.6400	0.350	0.111					
B5	M	10	7.0430	0.313	0.099	2.60	0.171	3.74	18	0.001
	F	10	6.3390	0.505	0.160					
B6	M	10	5.3390	0.442	0.140	1.62	0.484	4.14	18	0.001
	F	10	4.6030	0.347	0.110					
B7	M	10	3.2750	0.252	0.080	1.04	0.949	4.59	18	0.000
	F	10	2.7630	0.247	0.078					
B8	M	10	5.4400	0.415	0.131	1.59	0.499	1.99	18	0.062
	F	10	5.1070	0.329	0.104					
B9	M	10	6.1620	0.391	0.124	1.66	0.463	2.98	18	0.008
	F	10	5.6950	0.304	0.096					
B10	M	10	4.6310	0.461	0.146	1.53	0.539	4.15	18	0.001
	F	10	3.8520	0.373	0.118					
B11	M	10	3.1600	0.262	0.083	1.29	0.708	3.30	18	0.004
	F	10	2.7460	0.298	0.094					
B12	M	10	6.8700	0.668	0.211	3.23	0.095	5.62	18	0.000
	F	10	5.5100	0.372	0.118					

* value for males and females

TABLE 5.23: GORILLA: SUMMARY STATISTICS: BASE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B13	M	10	4.1050	0.348	0.110	1.14	0.851	6.09	18	0.000
	F	10	3.1850	0.327	0.103					
B14	M	10	7.4800	0.797	0.252	1.95	0.332	5.02	18	0.000
	F	10	5.9250	0.570	0.180					
B15	M	10	3.6070	0.272	0.086	2.09	0.286	4.73	18	0.000
	F	10	2.8920	0.393	0.124					
B16	M	10	13.2570	0.953	0.301	1.12	0.868	7.34	18	0.000
	F	10	10.0340	1.009	0.319					
B17	M	10	16.1770	0.524	0.166	2.47	0.193	10.09	18	0.000
	F	10	13.0620	0.824	0.260					
B18	M	10	12.2210	0.715	0.226	1.40	0.627	6.37	18	0.000
	F	10	10.3350	0.605	0.191					
B19	M	10	8.2710	0.587	0.186	1.07	0.921	5.83	18	0.000
	F	10	6.7680	0.567	0.179					
B20	M	10	13.2500	1.253	0.396	2.38	0.212	9.11	18	0.000
	F	10	8.9500	0.811	0.257					
B21	M	10	5.1650	0.444	0.140	1.21	0.780	5.17	18	0.000
	F	10	4.0860	0.489	0.154					
B22	M	10	8.3120	0.740	0.234	2.85	0.134	6.26	18	0.000
	F	10	6.6080	0.438	0.139					
B23	M	10	0.7080	0.328	0.104	3.03	0.114	2.17	18	0.044
	F	10	0.4490	0.188	0.059					
B24	M	10	1.2980	0.315	0.100	2.94	0.124	0.60	18	0.557
	F	10	1.2290	0.184	0.058					

* value for males and females

CV are due to the combination of the sexes which are not especially variable when considered separately and the value of CV of B15 (basioccipital length) is caused by the high value of CV for females only. Male values range from 3.24 (B17) to 46.27 (B23), males are more variable than females in 13 cases (B1, B3, B4, B6, B8 - 10, B12, B14, B20, B22 - 24), and are more variable than the species in one instance (B24). Female values range from 4.11 (B3) to 41.88 (B23) and in no cases are they more variable than the species.

Sex differences in mean values

There is a significant difference between the means of male and female values in 22 cases (all but B8 and B24) at the 5 per cent level or less (see table 5.23). Percentage sexual dimorphism has a range of 63.4 (B23) to 94.7 % (B24) (see table 5.09). B23 is a small measurement and although there is a large overlap of male and female ranges the difference in the means is magnified but for B24 there is almost a total overlap of ranges with male values more dispersed than those of the females. The mean value of percentage sexual dimorphism for the base is 83 %. The main cause of difference between males and females in measurements of the base is size.

5.5.4 Vault

Sex differences in variance

There are 11 cases where there is a significant difference between the variances of male and female values at the 5 % level or less (V1, V7, V11-15, V18 - 21) (see table 5.24). The values of CV for the species range from 5.95 (V1) to 54.80 (V12) (see table 5.11). V11 and V12 (inion chord and arc) are highly variable for the same reasons as given above for *Pan.* V13 and V14 (nuchal chord and arc) are more variable for males and may be affected by the presence of the temporal/nuchal crest. V5, V6, and V8 (parietal arc and chord, and occipital chord) are also more variable for males and may be affected by the presence of the sagittal crest while V23 and V24 are variable for the reasons given previously for *H. sapiens.* The combination of male and female values causes the variability for V3, V15, V16, V20, and V21 which are not variable for the sexes when considered separately. Males values range from 2.72 (V22) to 35.01 (V7). Males are more variable than females in 15 cases (V1, V2, V7 - 11, V13 - 16, V18 - 21) and are more variable than the species in 4 cases (V1, V2, V7, V10). Female values range from 2.65 (V15) to 30.69 (V11) and females are more variable than the species in two traits (V5, V6) which are related to the position of inion. The shape of the vault is affected by the temporal and nuchal muscles and accounts for the difference in variance between the sexes in the above measurements.

TABLE 5.24: GORILLA: SUMMARY STATISTICS: VAULT

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V1	M	10	8.2690	0.611	0.193	4.93	0.026	1.34	18	0.196
	F	10	7.9850	0.275	0.087					
V2	M	10	10.4750	0.798	0.252	2.95	0.123	0.63	18	0.535
	F	10	10.2900	0.465	0.147					
V3	M	10	11.0200	1.060	0.335	1.07	0.921	4.96	18	0.000
	F	10	8.7050	1.025	0.324					
V4	M	10	9.2550	0.848	0.268	1.11	0.875	3.63	18	0.002
	F	10	7.8390	0.895	0.283					
V5	M	10	7.6900	1.075	0.340	1.38	0.638	0.25	18	0.807
	F	10	7.5600	1.264	0.400					
V6	M	10	7.3790	0.954	0.302	1.64	0.473	0.44	18	0.667
	F	10	7.1650	1.221	0.386					
V7	M	9	9.2111	3.225	1.075	13.65	0.001	1.45	17	0.166
	F	10	7.6800	0.873	0.276					
V8	M	9	7.0800	0.637	0.212	2.21	0.260	2.93	17	0.009
	F	10	6.3580	0.429	0.136					
V9	M	10	10.6950	0.566	0.179	2.04	0.303	4.76	18	0.000
	F	10	9.6550	0.396	0.125					
V10	M	10	6.0330	0.526	0.166	1.21	0.777	1.21	18	0.244
	F	10	5.7620	0.478	0.151					
V11	M	10	3.5370	1.117	0.353	4.19	0.044	4.47	18	0.000
	F	10	1.7790	0.546	0.173					
V12	M	10	5.5800	1.527	0.483	6.50	0.010	6.69	18	0.000
	F	10	2.1100	0.599	0.189					

* value for males and females

TABLE 5.24: GORILLA: SUMMARY STATISTICS: VAULT CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V13	M	9	8.4544	1.604	0.535	14.83	0.000	5.88	17	0.000
	F	10	5.3680	0.417	0.132					
V14	M	9	8.7444	1.683	0.561	15.62	0.000	5.92	17	0.000
	F	10	5.4950	0.426	0.135					
V15	M	10	11.8650	0.608	0.192	6.44	0.011	13.67	18	0.000
	F	10	9.0390	0.240	0.076					
V16	M	10	39.2300	2.873	0.908	2.61	0.169	10.74	18	0.000
	F	10	27.7500	1.778	0.562					
V17	M	10	13.7660	0.547	0.173	1.11	0.881	9.22	18	0.000
	F	10	11.5670	0.519	0.164					
V18	M	10	11.5950	0.835	0.264	5.48	0.018	5.69	18	0.000
	F	10	9.9620	0.357	0.113					
V19	M	10	11.4060	0.878	0.278	4.46	0.036	5.73	18	0.000
	F	10	9.6440	0.416	0.132					
V20	M	10	11.2210	0.992	0.314	9.69	0.002	7.61	18	0.000
	F	10	8.7120	0.319	0.101					
V21	M	10	19.6850	1.678	0.531	7.11	0.007	7.32	18	0.000
	F	10	15.5400	0.629	0.199					
V22	M	10	14.3850	0.392	0.124	1.96	0.330	11.22	18	0.000
	F	10	11.9940	0.549	0.173					
V23	M	10	2.1270	0.468	0.148	1.35	0.665	2.76	18	0.013
	F	10	1.5880	0.403	0.128					
V24	M	10	2.2350	0.272	0.086	1.53	0.535	4.35	18	0.000
	F	10	1.6390	0.337	0.107					

* value for males and females

Sex differences in mean values

In 18 cases there is a significant difference between the means of male and female values (V3, V4, V8, V9, V11 - 24) at the five per cent level or less (see table 5.24). Percentage sexual dimorphism has a range of 37.8 (V12) to 98.3 (V5) % (see table 5.12). The ranges of males and females for V12 (inion arc) overlap slightly with male values more dispersed than female values and for V5 (parietal arc) the ranges overlap completely. The mean value of percentage sexual dimorphism for the vault is 79.9 %. The effects of the temporal and nuchal muscles account for differences in the shape of the skulls of the male and female *Gorilla* but the overall size difference between the sexes accounts for the difference in mean values of the vault measurements.

5.5.5 Face

Sex differences in variance

In nine cases there is a significant difference between the variance of males and females at the five per cent level or less (F3, F8, F12, F13, F16, F18, F22, F23, F25) (see table 5.25). F3 (orbit breadth) and F8 (upper facial breadth) may be affected by the size of the supraorbital region which in males is large due to the need for large temporal muscle attachment area and F18 (superior malar length) and F23 (lateral facial length) would also be affected by the size of the masticatory muscles. F22 (superior facial length) and F25 (basi-alveolar length) are correlated with the angle of the basicranium and the length of the palate which in turn would affect F12 (upper facial height).

The values of CV for the species range from 7.88 (F3) to 39.52 (F15) (see table 5.14). F15, F16, F26, and F27 are highly variable for the reasons stated above for *H. sapiens.* For F2 (interorbital breadth) and F5 (glabella projection) both sexes are slightly variable which results in high values of CV when they are combined whereas F13 (nasal height) is variable for males but not females and F10 (zygomaxillary subtense) is not variable for the sexes separately. Male values range from 3.53 (F6) to 35.64 (F16), males are more variable than females in 21 cases (F1 - 4, F6 - 14, F16 - 19, F22, F23, F25, F26), and males are more variable than the species in one case (F13). Female values range from 3.04 (F8) to 50.32 (F15) and females are more variable than the species in one case (F15).

Sex differences in mean values

In all but 2 cases (F4 -orbital height, F15 -simotic chord) there is a significant difference between the means of male and female values at the 5 per cent level or

TABLE 5.25: GORILLA: SUMMARY STATISTICS: FACE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F1	M	10	11.4540	0.582	0.184	2.37	0.215	7.67	18	0.000
	F	10	9.7720	0.378	0.119					
F2	M	10	2.4900	0.378	0.119	2.17	0.263	5.15	18	0.000
	F	10	1.7470	0.256	0.081					
F3	M	10	4.5240	0.323	0.102	5.78	0.015	4.20	18	0.001
	F	10	4.0600	0.134	0.042					
F4	M	10	4.2610	0.350	0.111	1.60	0.497	2.04	18	0.056
	F	10	3.9730	0.277	0.088					
F5	M	10	2.5720	0.281	0.089	1.17	0.819	7.33	18	0.000
	F	10	1.6860	0.259	0.082					
F6	M	10	14.8900	0.526	0.166	1.68	0.451	12.01	18	0.000
	F	10	12.3690	0.405	0.128					
F7	M	10	17.4100	0.791	0.250	2.73	0.150	12.45	18	0.000
	F	10	13.7700	0.479	0.151					
F8	M	10	12.3470	0.854	0.270	7.45	0.006	7.20	18	0.000
	F	10	10.2770	0.313	0.099					
F9	M	10	12.7510	0.856	0.271	2.18	0.262	5.83	18	0.000
	F	10	10.8470	0.580	0.183					
F10	M	10	5.3400	0.550	0.174	1.97	0.329	5.66	18	0.000
	F	10	4.1300	0.392	0.124					
F11	M	10	8.3180	0.668	0.211	2.29	0.233	6.20	18	0.000
	F	10	6.7500	0.441	0.140					
F12	M	10	12.5850	1.489	0.471	18.08	0.000	4.01	18	0.001
	F	10	10.6440	0.350	0.111					
F13	M	10	10.7720	1.642	0.519	28.43	0.000	3.51	18	0.002
	F	10	8.9150	0.308	0.097					

* value for males and females

TABLE 5.25: GORILLA: SUMMARY STATISTICS: FACE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F14	M	10	3.7790	0.386	0.122	2.31	0.228	2.76	18	0.013
	F	10	3.3760	0.254	0.080					
F15	M	10	0.6930	0.202	0.064	1.72	0.437	1.56	17	0.137
	F	9	0.5256	0.264	0.088					
F16	M	10	1.1080	0.395	0.125	10.45	0.002	2.92	18	0.009
	F	10	0.7260	0.122	0.039					
F17	M	10	12.5250	0.841	0.266	2.63	0.165	5.70	18	0.000
	F	10	10.7440	0.518	0.164					
F18	M	10	7.1660	0.774	0.245	9.05	0.003	4.46	18	0.000
	F	10	6.0160	0.257	0.081					
F19	M	10	8.2210	0.850	0.269	2.05	0.301	4.40	18	0.000
	F	10	6.7780	0.594	0.188					
F20	M	10	6.4980	0.434	0.137	1.28	0.722	11.45	18	0.000
	F	10	4.4020	0.384	0.121					
F21	M	10	4.5540	0.354	0.112	1.24	0.750	7.63	18	0.000
	F	10	3.4050	0.318	0.100					
F22	M	10	19.2950	1.585	0.501	4.56	0.034	7.06	18	0.000
	F	10	15.3870	0.742	0.235					
F23	M	10	10.0430	1.063	0.336	16.81	0.000	4.58	18	0.000
	F	10	8.4590	0.259	0.082					
F24	M	10	14.1570	0.813	0.257	1.14	0.844	6.49	18	0.000
	F	10	11.8750	0.759	0.240					
F25	M	9	19.6456	1.746	0.582	4.94	0.028	6.85	17	0.000
	F	10	15.4680	0.785	0.248					
F26	M	10	1.8380	0.262	0.083	2.83	0.137	3.58	18	0.002
	F	10	1.4930	0.155	0.049					
F27	M	10	0.8530	0.158	0.050	1.70	0.441	4.85	18	0.000
	F	10	0.5480	0.121	0.038					

* value for males and females

less, probably due to a difference in overall size between the sexes (see table 5.25). Percentage sexual dimorphism ranges from 64.2 (F27) to 93.2 % (F4) (see table 5.15). F27 is a small measurement so any difference between the means is amplified but for F4 the ranges of the values for males and females overlap considerably. The mean value of percentage sexual dimorphism is 79.9 %.

5.5.6 Overall Effect On Cranium

The differences between the variances and means of the sexes are caused by the effects of size and shape. A large mandible would have the same effect as discussed for *Pan* but the effects of the temporal and nuchal muscles account for the majority of shape difference in the vault and facial areas. Thus the fact that males are larger than females would account for much of the difference in the means but the greater size of the male *Gorilla* skull has ramifications in terms of shape differences between the sexes.

In comparison to *Pan*, *Gorilla* has more characters in the face and vault regions where there is a significant difference between the variances of males and females. Also, in contrast to *Pan*, *Gorilla* males possess more characters with values of CV higher than in females. The fact that *Gorilla* is more dimorphic than *Pan* is reflected not only in the number of characters where there is a significant difference between the means of the sexes but also in the mean percentage sexual dimorphism per region, the values of which are about 10% or more less than those of *Pan*. In *Gorilla*, as in *Pan*, the palate is the least dimorphic region but the face and vault are the most dimorphic in *Gorilla*. Finally *Gorilla* has a larger range of values of percentage sexual dimorphism than does *Pan*.

5.6 Pongo

5.6.1 Mandible

Sex differences in variance

The variances of the male and female values are significantly different in 4 cases (M1 - 3, M8) which are measurements of breadth and total length (see table 5.26). The values of CV for the species range from 6.45 (M9) to 15.29 (M4) (see table 5.02). Male values range from 3.79 (M12) to 13.59 (M7) with males more variable than females in nine cases (M1 - 4, M6 - 9, M11) and having a higher value of CV than the species in three cases (M2, M7, M8). Female values of CV range from 3.91 (M9) to 11.64 (M5) and in all cases the female values of CV are less than for the species. Thus neither sex is particularly variable in mandibular traits though there is a significant

TABLE 5.26: PONGO: SUMMARY STATISTICS: MANDIBLE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
M1	M	10	10.4630	1.372	0.434	4.93	0.026	3.55	18	0.002
	F	10	8.7730	0.617	0.195					
M2	M	10	5.0110	0.638	0.202	7.02	0.008	3.03	18	0.007
	F	10	4.3580	0.241	0.076					
M3	M	10	15.0150	1.311	0.415	4.41	0.038	5.64	18	0.000
	F	10	12.4250	0.624	0.197					
M4	M	10	6.0190	0.676	0.214	2.87	0.132	4.92	18	0.000
	F	10	4.7980	0.399	0.126					
M5	M	10	4.8700	0.525	0.166	1.24	0.753	3.68	18	0.002
	F	10	4.0480	0.471	0.149					
M6	M	10	9.8770	1.082	0.342	3.34	0.087	4.05	18	0.001
	F	10	8.2970	0.593	0.187					
M7	M	10	2.4730	0.336	0.106	3.37	0.085	1.78	18	0.091
	F	10	2.2570	0.183	0.058					
M8	M	10	4.4800	0.376	0.119	4.28	0.041	1.32	18	0.202
	F	10	4.3050	0.182	0.057					
M9	M	10	6.4110	0.308	0.097	1.82	0.387	4.73	18	0.000
	F	10	5.8380	0.228	0.072					
M10	M	10	3.8800	0.330	0.104	1.19	0.804	3.70	18	0.002
	F	10	3.3550	0.303	0.096					
M11	M	10	3.9530	0.446	0.141	1.56	0.517	3.48	18	0.003
	F	10	3.3250	0.357	0.113					
M12	M	10	8.5130	0.323	0.102	1.10	0.887	7.26	18	0.000
	F	10	7.4380	0.339	0.107					
	*	value	for	males	and	females				

difference between the variances of the sexes in some measures of breadth and total length.

Sex differences in mean values

In ten cases the means of males and females are significantly different at the one per cent level or less (M1 - 6, M9 - 12) (see table 5.26). Percentage sexual dimorphism ranges from 79.7 (M4) to 96.1 (M8) (see table 5.03). For M4 (ramus breadth) the ranges of male and female values only slightly overlap and for M8 (internal breadth) the male range overlaps the female one considerably. The mean value of percentage sexual dimorphism for the mandible is 86.4 %. The reason for the difference between the means of the sexes is likely due to size.

5.6.2 Palate

Sex differences in variance

The variances of males and females for P9 (bicanine breadth) are significantly different (p=0.01) (see table 5.27). The difference between the variances of the sexes for bicanine breadth is caused by the variability of the male sample as females are less than half as variable as males for this measurement.

Values of CV for the species range from 7.55 (P5) to 26.43 (P7) (see table 5.05) where P7 and P8 are highly variable as in the previous species. Male values range from 3.64 (P5) to 22.33 (P7) with males more variable than females in 6 cases (P1 - 4, P6, P9) and as variable as the species in one case (P9). Female values of CV range from 4.00 (P6) to 23.50 (P7) and in all cases they are less than the values of CV for the species.

Sex differences in mean values

In all cases there is a significant difference between the means of the male and female values at the 5 per cent level or less (see table 5.27). Percentage sexual dimorphism has a range of 71.6 (P8) to 89.0 (P4) % (see table 5.06). P8 is a small measurement so the difference between the means is accentuated and the ranges of male and female values for P4 (external breadth) overlap slightly but most male values are greater than those for the females. The mean value of percentage sexual dimorphism for the palate is 84.1 %. *Pongo* is very dimorphic in the palate which accounts for the significant difference in the mean values of all mandibular traits for the sexes.

TABLE 5.27: PONGO: SUMMARY STATISTICS: PALATE

VAR	SEX	NO. OF CASES	MEAN	STD DEV.	STD ERR.	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
P1	M	10	8.1220	0.573	0.181	1.90	0.351	5.97	18	0.000
	F	10	6.7870	0.415	0.131					
P2	M	10	4.2450	0.419	0.133	2.24	0.244	3.22	18	0.005
	F	10	3.7320	0.280	0.089					
P3	M	10	8.9940	0.519	0.164	1.80	0.396	5.86	18	0.000
	F	10	7.7950	0.387	0.122					
P4	M	10	7.1880	0.490	0.155	3.09	0.108	4.44	18	0.000
	F	10	6.3960	0.279	0.088					
P5	M	10	8.9340	0.325	0.103	1.11	0.872	6.96	17	0.000
	F	9	7.8667	0.343	0.114					
P6	M	9	7.0456	0.415	0.138	2.75	0.153	5.10	17	0.000
	F	10	6.2540	0.250	0.079					
P7	M	10	1.8400	0.411	0.130	1.57	0.512	2.67	18	0.016
	F	10	1.3960	0.328	0.104					
P8	M	10	1.8140	0.274	0.087	1.62	0.485	4.67	18	0.000
	F	10	1.2990	0.216	0.068					
P9	M	10	4.2380	0.572	0.181	5.69	0.016	3.12	18	0.006
	F	10	3.6270	0.240	0.076					

* value for males and females

5.6.3 Base

Sex differences in variance

In 6 cases the variances of males and females are significantly different at the 5 % level or less (B14, B19 - 23) (see table 5.28). The difference between the variances of the sexes occurs in two areas of the skull: the nuchal region (B19, B20); and the basicranial axis (B14, B21, B22, B23).

The values of CV range from 7.16 (B4) to 37.14 (B24) for the species (see table 5.08) where B24 is variable for males and females, B23 for males but not females, and for B13 (biforamen ovale line-bitympanic line) and B20 - 22 (lateral nuchal crest arc, sphenooccipital synchrondosis-staphlyon chord, staphlyon-basion chord) males contribute more to the variability of the species than do females. Male values of CV range from 7.03 (B4) to 42.44 (B24) with male values of CV greater than those of the species in six cases (B1, B9, B15, B19, B20, B24). Female values of CV range from 3.60 (B20) to 30.98 (B24) with female values greater than male and species values in three cases (B1, B2, B7). Males and females both have higher values of CV than the species for B1 (foramen magnum length).

Sex differences in mean values

In 19 cases the means of the male and female values are significantly different at the 5 per cent level or less (B3 - 6, B8, B10 - 23) (see table 5.28) and percentage sexual dimorphism has a range of 75.5 (B23) to 99.3 (B2) % (see table 5.09). The ranges of male and female values for B23 (articular eminence height) overlap but the upper range of the males has the larger values whereas for B2 (foramen magnum length) females are more variable than males and their range totally overlaps the male range. The mean value of percentage sexual dimorphism for the base is 88.0 %. The difference in mean values is mainly due to size differences between the sexes.

5.6.4 Vault

Sex differences in variance

There are four cases where the variances of male and female values are significantly different at the 5 per cent level or less (V13, V15, V16, V21) (see table 5.29). These characters are associated with the nuchal area (V13), the size of the temporal muscle (V15, V16) and the total length of the skull (V21). For V21 the male value of CV is twice that of the females but both sexes have low values of CV.

The values of CV range from 5.61 (V21) to 32.67 (V12) (see table 5.11). V11,

TABLE 5.28: PONGO: SUMMARY STATISTICS: BASE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B1	M	10	3.1830	0.376	0.119	1.01	0.987	0.58	18	0.566
	F	10	3.0850	0.374	0.118					
B2	M	10	2.5590	0.173	0.055	2.99	0.123	0.16	17	0.873
	F	9	2.5411	0.298	0.099					
B3	M	10	12.1380	0.961	0.304	2.62	0.168	4.22	18	0.001
	F	10	10.6300	0.594	0.188					
B4	M	10	7.6880	0.540	0.171	1.81	0.389	2.39	18	0.028
	F	10	7.1790	0.401	0.127					
B5	M	10	6.7860	0.549	0.174	1.47	0.573	2.56	18	0.020
	F	10	6.2090	0.452	0.143					
B6	M	10	5.1860	0.474	0.150	3.82	0.059	3.30	18	0.004
	F	10	4.6290	0.243	0.077					
B7	M	10	2.8530	0.210	0.066	1.22	0.774	1.76	18	0.095
	F	10	2.6790	0.232	0.073					
B8	M	10	4.6370	0.333	0.105	1.62	0.486	3.04	18	0.007
	F	10	4.2290	0.262	0.083					
B9	M	10	5.4540	0.564	0.178	1.85	0.373	1.43	18	0.171
	F	10	5.1380	0.415	0.131					
B10	M	10	3.5610	0.332	0.105	1.47	0.577	3.16	18	0.005
	F	10	3.1310	0.274	0.087					
B11	M	10	2.9930	0.251	0.079	1.45	0.586	4.05	18	0.001
	F	10	2.5750	0.208	0.066					
B12	M	10	6.1350	0.574	0.182	1.51	0.552	4.61	18	0.000
	F	10	5.0550	0.468	0.148					

* value for males and females

TABLE 5.28: PONGO: SUMMARY STATISTICS: BASE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
B13	M	10	3.0350	0.436	0.138	2.91	0.127	3.64	18	0.002
	F	10	2.4530	0.255	0.081					
B14	M	10	6.4300	0.680	0.215	7.58	0.006	4.33	18	0.000
	F	10	5.4400	0.247	0.078					
B15	M	10	2.9670	0.370	0.117	3.91	0.055	2.52	18	0.021
	F	10	2.6370	0.187	0.059					
B16	M	10	11.7740	1.198	0.379	2.18	0.262	3.39	18	0.003
	F	10	10.2220	0.812	0.257					
B17	M	10	13.8900	1.311	0.415	2.83	0.137	4.02	18	0.001
	F	10	11.9510	0.779	0.246					
B18	M	10	10.9330	0.999	0.316	3.16	0.102	3.46	18	0.003
	F	10	9.6770	0.562	0.178					
B19	M	10	7.0730	0.738	0.233	4.17	0.045	3.00	18	0.008
	F	10	6.2930	0.361	0.114					
B20	M	10	9.3530	1.488	0.471	26.61	0.000	2.80	18	0.012
	F	10	8.0100	0.288	0.091					
B21	M	10	4.9830	0.618	0.195	5.68	0.016	4.52	18	0.000
	F	10	4.0240	0.259	0.082					
B22	M	10	7.8380	0.935	0.296	7.77	0.005	4.66	18	0.000
	F	10	6.3730	0.336	0.106					
B23	M	10	0.8570	0.216	0.068	6.67	0.009	2.87	18	0.010
	F	10	0.6470	0.084	0.026					
B24	M	10	0.8240	0.350	0.111	2.30	0.230	0.60	18	0.553
	F	10	0.7440	0.231	0.073					

* value for males and females

TABLE 5.29: PONGO: SUMMARY STATISTICS: VAULT

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V1	M	10	7.7300	0.468	0.148	1.31	0.698	1.52	18	0.145
	F	10	7.3880	0.535	0.169					
V2	M	10	9.9650	0.690	0.218	3.03	0.114	1.63	18	0.121
	F	10	9.5550	0.397	0.125					
V3	M	10	7.2450	0.775	0.245	1.51	0.551	1.22	18	0.239
	F	10	6.8600	0.631	0.200					
V4	M	10	6.9000	0.612	0.194	1.21	0.781	1.61	18	0.126
	F	10	6.4800	0.556	0.176					
V5	M	10	6.5950	0.463	0.147	2.41	0.206	2.67	18	0.016
	F	10	6.1300	0.298	0.094					
V6	M	10	6.3350	0.391	0.124	2.07	0.292	3.10	18	0.006
	F	10	5.8680	0.272	0.086					
V7	M	10	7.5500	0.862	0.273	2.26	0.241	2.47	18	0.024
	F	10	6.7400	0.574	0.181					
V8	M	10	6.1600	0.687	0.217	1.61	0.487	2.23	18	0.039
	F	10	5.5430	0.541	0.171					
V9	M	10	9.8380	0.723	0.229	3.00	0.118	2.36	18	0.030
	F	10	9.2160	0.418	0.132					
V10	M	10	5.3090	0.275	0.087	2.22	0.251	1.17	18	0.258
	F	10	5.1270	0.409	0.129					
V11	M	10	1.9850	0.480	0.152	2.31	0.228	0.19	18	0.850
	F	10	1.9320	0.731	0.231					
V12	M	10	2.3600	0.624	0.197	1.74	0.422	0.86	18	0.403
	F	10	2.0800	0.823	0.260					

* value for males and females

TABLE 5.29: PONGO: SUMMARY STATISTICS: VAULT CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
V13	M	10	4.8310	0.868	0.275	5.10	0.024	1.59	18	0.128
	F	10	4.3520	0.385	0.122					
V14	M	10	5.2600	0.755	0.239	1.64	0.470	2.12	18	0.049
	F	10	4.6200	0.588	0.186					
V15	M	10	9.4080	1.398	0.442	6.47	0.010	3.74	18	0.001
	F	10	7.6310	0.550	0.174					
V16	M	10	25.1800	3.509	1.110	4.09	0.048	3.76	18	0.001
	F	10	20.5200	1.734	0.548					
V17	M	10	11.5770	1.054	0.333	2.12	0.280	3.70	18	0.002
	F	10	10.0820	0.725	0.229					
V18	M	10	9.1140	0.764	0.242	3.29	0.090	3.23	18	0.005
	F	10	8.2220	0.421	0.133					
V19	M	10	8.9530	0.725	0.229	2.40	0.209	3.95	18	0.001
	F	10	7.8750	0.468	0.148					
V20	M	10	9.4920	1.071	0.339	2.73	0.151	3.98	18	0.001
	F	10	7.9150	0.649	0.205					
V21	M	10	13.1700	0.673	0.213	5.21	0.022	4.20	18	0.001
	F	10	12.1950	0.295	0.093					
V22	M	10	12.7950	1.131	0.358	2.59	0.173	3.91	18	0.001
	F	10	11.1470	0.703	0.222					
V23	M	10	1.2980	0.367	0.116	1.14	0.850	1.55	18	0.139
	F	10	1.0520	0.344	0.109					
V24	M	10	1.6240	0.212	0.067	2.69	0.157	2.28	18	0.035
	F	10	1.3310	0.347	0.110					

* value for males and females

V12, V23, and V24 are variable for the reasons given previously, although for V24 males are half as variable as females. V15 and V16 (height and arc of temporal muscle mark) are more variable for males because the temporal muscle in males migrates further upward than in females and the high value of CV for V13 (nuchal chord) is caused by the fact that the male values are considerably dispersed for this variable. Male values of CV range from 5.11 (V21) to 28.26 (V23) with males more variable than females in 18 cases (V2 - 9, V13 - 22) and having a higher value than the species in four cases (V2, V3, V9, V13). Female values range from 2.42 (V21) to 39.57 (V12) with higher values than the species in six cases (V1, V10 - 12, V23, V24).

Sex differences in mean values

In fifteen cases there is a significant difference between the means of males and females at the 5 per cent level or less (V5 - 9, V14 - 22, V24) (see table 5.29). Percentage sexual dimorphism has a range of 81.0 (V23) to 97.3 (V11) % (see table 5.12). V23 is a small measurement so any difference between the means has a greater effect on the percentage sexual dimorphism and the ranges of male and female values overlap considerably for V11 (inion chord). The mean value of percentage sexual dimorphism for the vault is 89.7 %.

5.6.5 Face

Sex differences in variance

There are nine cases where the variances of male and female values are significantly different at the five per cent level or less (F2, F3, F9, F20 - 22, F24, F25, F27) (see table 5.30). F2, F3, and F9 are width measurements, F21 a measure of height, and the remainder length measurements. These latter measurements are related to prognathism and accord with the analysis of the base where traits affecting the basicranial angle are variable.

The values of CV for the species range from 6.59 (F4) to 63.79 (F15) (see table 5.14). The reasons for the high value of CV for F2, F5, F15, F16, F26, and F27 have been discussed previously. The high species value of CV for F10 (zygomaxillary subtense), F12 - 14 (upper facial height, nasal height and breadth), F18 (superior malar length), and F19 (maximum malar length) are due to the combination of the sexes which have lower values of CV alone. The value for F20 (inferior malar length) is caused by the large dispersion of male values and the value for F21 (minimum cheek height) is caused by the combination of male and female values which are both variable separately. Male values of CV range from 6.11 (F4) to 56.28 (F15) with larger values than females in all but two cases (F14, F26) and larger values than the

TABLE 5.30: PONGO: SUMMARY STATISTICS: FACE

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F1	M	10	8.7130	0.579	0.183	3.25	0.094	5.45	18	0.000
	F	10	7.5720	0.321	0.101					
F2	M	10	1.6420	0.387	0.123	4.43	0.037	3.33	18	0.004
	F	10	1.1910	0.184	0.058					
F3	M	10	3.7080	0.343	0.108	4.23	0.043	3.39	18	0.003
	F	10	3.3000	0.167	0.053					
F4	M	10	4.0350	0.247	0.078	1.78	0.403	2.89	18	0.010
	F	10	3.7530	0.185	0.058					
F5	M	10	0.3390	0.169	0.053	3.41	0.082	0.87	18	0.394
	F	10	0.2860	0.091	0.029					
F6	M	10	11.4160	1.095	0.346	3.37	0.085	4.17	18	0.001
	F	10	9.7730	0.597	0.189					
F7	M	10	15.7540	1.805	0.571	3.09	0.108	4.03	18	0.001
	F	10	13.1110	1.026	0.324					
F8	M	10	9.5130	0.826	0.261	2.83	0.137	4.72	18	0.000
	F	10	8.0790	0.491	0.155					
F9	M	10	11.4540	1.246	0.394	4.91	0.027	3.57	18	0.002
	F	10	9.9110	0.562	0.178					
F10	M	10	4.0030	0.524	0.166	1.83	0.383	4.17	18	0.001
	F	10	3.1430	0.388	0.123					
F11	M	10	7.0100	0.635	0.201	2.50	0.188	4.75	18	0.000
	F	10	5.8810	0.402	0.127					
F12	M	10	10.0790	1.312	0.415	2.07	0.293	4.11	18	0.001
	F	10	8.0040	0.911	0.288					
F13	M	10	7.6180	0.805	0.254	1.49	0.526	4.21	18	0.001
	F	10	6.2330	0.659	0.208					

* value for males and females

TABLE 5.30: PONGO: SUMMARY STATISTICS: FACE CONT'D

VAR	SEX	NO. OF CASES	MEAN	STDDEV	STDER	F VALUE *	2-TAIL PROB. *	T VALUE *	DEG. FR. *	2-TAIL PROB. *
F14	M	10	3.3420	0.271	0.086	2.00	0.317	3.38	18	0.003
	F	10	2.8400	0.384	0.121					
F15	M	10	0.3000	0.169	0.053	3.26	0.111	2.09	17	0.052
	F	9	0.1667	0.094	0.031					
F16	M	10	0.9100	0.243	0.077	1.82	0.387	-0.01	18	0.992
	F	10	0.9110	0.180	0.057					
F17	M	10	10.4920	0.888	0.281	2.73	0.151	3.72	18	0.002
	F	10	9.2720	0.537	0.170					
F18	M	10	6.0850	0.630	0.199	1.81	0.389	3.97	18	0.001
	F	10	5.0990	0.468	0.148					
F19	M	10	6.0380	0.720	0.228	1.96	0.331	3.91	18	0.001
	F	10	4.9450	0.515	0.163					
F20	M	10	4.8890	0.932	0.295	4.30	0.041	3.88	18	0.001
	F	10	3.6210	0.449	0.142					
F21	M	10	3.9210	0.608	0.192	2.17	0.263	4.63	18	0.000
	F	10	2.8470	0.412	0.130					
F22	M	10	16.3380	1.434	0.454	6.19	0.012	6.12	18	0.000
	F	10	13.3470	0.577	0.182					
F23	M	10	8.0110	0.573	0.181	1.50	0.559	3.88	18	0.001
	F	10	7.1030	0.468	0.148					
F24	M	10	10.1300	0.914	0.289	6.16	0.012	2.70	18	0.015
	F	10	9.2880	0.368	0.116					
F25	M	10	16.5260	1.435	0.454	4.20	0.044	5.60	18	0.000
	F	10	13.6960	0.701	0.222					
F26	M	10	1.6650	0.271	0.086	1.36	0.655	3.81	18	0.001
	F	10	1.2350	0.232	0.074					
F27	M	10	0.7810	0.230	0.073	6.00	0.014	4.07	18	0.001
	F	10	0.4620	0.094	0.030					

* value for males and females

species in three cases (F5, F16, F24). Females values range from 3.97 (F24) to 56.12 (F15).

Sex differences in mean values

There is a significant difference between the male and female means in 24 cases (F1 - 4, F6 - 14, F17 - 27) at the five per cent level or less (see table 5.30). *Pongo* is highly dimorphic in most of the measurements of the face due to size differences between the sexes. Other differences in shape are due to the effects of the masticatory system on the vault, basicranium, and face.

Percentage sexual dimorphism has a range of 55.7 (F15) to 100.1 (F16) % (see table 5.15). F15 (simotic chord) is a small measurement so although the male range totally overlaps the female range the difference between the means is magnified. With respect to F16, both sexes are variable for this character and their ranges overlap considerably so, although their means are similar in this sample, the female mean is greater than the male mean. The mean value of percentage sexual dimorphism is 81.8 %.

5.6.6 Overall Effect On Cranium

The intercorrelations of traits for *Pongo* are common to all four species: the basicranial axis affects facial prognathism; the size of the mandible affects the base of the skull and determines the size of the masticatory and nuchal muscles. The effect of these factors on the shape of the skull is determined by size; the larger the mandible the greater the effect on skull shape. Thus the effects of these factors are more pronounced in *Gorilla* and *Pongo* and especially so in the males of these species.

An examination of mean percentage sexual dimorphism shows *Gorilla* to be more dimorphic than *Pongo* but these two species are more dimorphic in more characters than are *Pan* and *H. sapiens.* With *Pan* and *H. sapiens* there is less of a difference between the sexes with respect to their means and variances and females possess greater values of CV for more characters than do males. In *Pongo* and *Gorilla* males have higher values of CV in more characters than do females. But an overview of the values of mean percentage sexual dimorphism per region shows that the patterns of dimorphism differ between all these modern groups.

In all four modern groups there are some common regions containing characters that are variable and dimorphic including the areas of the temporal and nuchal muscle attachment, area of basicranial kyphosis, width measurements of the palate, mandible, and base, and facial prognathism.

5.7 Homo erectus

5.7.1 Mandible

The values of CV range from 5.13 (M6) to 19.10 (M2 -foramen mentalia breadth) (see table 5.31). For M2 the measurement values range from 3.91cm (BL 8518) to 6.6cm (OH 22) and this measurement is obviously affected by the position of the foramena as well as the thickness and width of the mandible. The next highest value of CV is 14.40 for M8 (internal breadth).

5.7.2 Palate

The only measurements of the palate for which there were more than one individual to compare were P1, P3, P7 - P9 (see table 5.32). The values of CV are very high for P7 and P8 (palatal depth) where for P7, KNM-ER 3733 and SANGIRAN 17 have the same value (1.5cm) but OH 12 is much smaller (0.65cm) and for P8, KNM-ER 807 (1.96cm) and KNM-ER 3733 (1.35cm) are closest in value and SANGIRAN 17 is much smaller (0.75cm).

5.7.3 Base

The values of CV for the base range from 4.77 (B3) to 52.49 (B23 -articular eminence height) (see table 5.33). B7 (bipetrous width) has a high value of CV (28.94) due to the measurement value of SANGIRAN 17 (5.4cm) which is larger than those of KNM-ER 3733, KNM-ER 3883, and OH 9 and B9 (biinfratemporal fossa width) has a large value of CV (16.72) for the same reason. For B20 (lateral nuchal crest arc) (CV=22.25) the measurement value of KNM-ER 3733 (9.5cm) is similar to those of the Asian specimens which range from 9.0cm to 11.0cm whereas KNM-ER 3883 (6.0cm), OH 9 (8.3cm), and OH 12 (5.0cm) have smaller measurement values. For B23 KNM-ER 3733 (.8cm) and KNM-ER 3883 (.85cm) have close measurement values whereas OH 9 (1.9cm) is more than twice their size. For B24 (CV=26.46) KNM-ER 3883 and OH 9 are closer in value than is KNM-ER 3733. The remaining measurements have lower values of CV.

5.7.4 Vault

The CV values for the vault range from 3.01 (V18) to 29.60 (V14 -nuchal arc) (see table 5.34). V5 and V6 (parietal arc and chord) (CV=16.29; 16.03) have the smallest measurement values on KNM-ER 3733, 3883, and Skull III, intermediate ones on Pithecanthropus I and II, Skull II, and Skull 3 (Locus E), and large ones of SANGIRAN 17 and Skull I. V11 - V14 (inion and nuchal arc and chord) are all highly variable due to the variation in the position of inion. For example, the position of

TABLE 5.31: FOSSIL VALUES OF CV: MANDIBLE

SP	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
H. erectus	7.64	19.10	7.20	12.40	11.77	5.13	11.88	14.40	6.86	12.24	11.64	6.51
H. habilis		7.12			22.73		25.64	4.65	6.29	15.19	5.33	12.03
A. afarensis	16.75	9.82	32.49	47.60	13.56	32.70	11.69	13.88	13.27	10.14	13.89	9.30
A. africanus	2.81	14.07	5.82	9.16	14.51	6.32	10.34	20.89	9.24	10.60	8.72	4.85
A. robustus			5.66	10.03	8.59	7.04	8.95			9.67	19.43	10.70
A. boisei	12.50	9.96	8.26	4.90	7.66	23.11	11.05	11.34	9.84	9.76	13.09	7.43

TABLE 5.32: FOSSIL VALUES OF CV: PALATE

SP	P1	P2	P3	P4	P5	P6	P7	P8	P9
H. erectus	2.90		8.32				40.35	44.72	1.05
H. habilis	8.76	6.49	9.03	13.06	9.27	9.79	22.31	8.57	15.67
A. afarensis	18.86	10.88	10.71	5.69	20.51	6.18	17.29		21.17
A. africanus	9.25	17.89	6.19	10.07	6.42	12.63	28.40	34.00	11.94
A. robustus	11.40	9.20	5.83	6.65	3.60	7.35	18.00	31.60	15.32
A. boisei	8.99	6.00	4.82	1.88	10.79	5.92	15.29	19.87	15.67

TABLE 5.33: FOSSIL VALUES OF CV: BASE

SP	B1	B2	B3	B4	B5	B6
H. erectus	12.72	11.16	4.77	6.21	7.83	7.77
H. habilis	4.26	4.20	15.83	7.06	7.57	13.00
A. afarensis						
A. africanus	4.88	11.64	3.28	1.53	3.36	7.73
A. robustus						
A. boisei	2.24	10.71	11.92	7.67	9.94	24.34
	B7	B8	B9	B10	B11	B12
H. erectus	28.94	5.34	16.72	5.82	8.11	4.80
H. habilis	6.72	20.15	12.18	21.14	23.35	14.35
A. afarensis						
A. africanus	30.75	7.27	4.55	4.04	8.67	11.45
A. robustus						
A. boisei	31.11	16.84	3.35	15.03	20.11	11.07
	B13	B14	B15	B16	B17	B18
H. erectus	10.83	5.98	10.77	6.07	5.38	7.05
H. habilis	28.10	16.43	15.28	7.76	12.25	7.45
A. afarensis				14.46		
A. africanus	22.27	11.23	10.83	4.68	6.18	5.07
A. robustus						
A. boisei	7.06	16.83	13.60	9.97	14.62	21.79
	B19	B20	B21	B22	B23	B24
H. erectus	10.77	22.25			52.49	26.46
H. habilis	5.99	5.83	1.19	24.23	7.25	20.69
A. afarensis		3.82			47.14	23.57
A. africanus	5.34	8.05	12.22	2.89	27.70	29.86
A. robustus			11.06	28.22	19.55	47.50
A. boisei	9.61	17.79	1.57	2.46	43.04	37.98

TABLE 5.34: FOSSIL VALUES OF CV: VAULT

SP	V1	V2	V3	V4	V5	V6
H. erectus	5.74	3.44	5.70	8.98	16.29	16.03
H. habilis	8.61	7.69	4.59	7.53	11.86	10.94
A. afarensis		8.50				
A. africanus	17.79	8.73	1.63	2.89	4.60	6.09
A. robustus						
A. boisei	3.19	7.44	21.18	22.69	6.11	4.34
	V7	V8	V9	V10	V11	V12
H. erectus	11.74	10.10	3.71	12.66	19.92	24.10
H. habilis	26.37	21.15	2.12	5.81	31.58	30.83
A. afarensis					1.10	2.11
A. africanus	4.48	7.13	7.60	21.21	22.49	11.62
A. robustus				35.00		
A. boisei	4.81	3.69	9.19	30.43	5.47	5.27
	V13	V14	V15	V16	V17	V18
H. erectus	26.54	29.60	3.79	10.20	5.39	3.01
H. habilis			15.32	13.20	17.20	11.55
A. afarensis						
A. africanus	44.54	44.20	2.22	1.52	11.17	10.46
A. robustus					1.94	
A. boisei	10.63	12.12	13.94	14.76	10.86	8.99
	V19	V20	V21	V22	V23	V24
H. erectus	6.77	9.47	5.88	6.03	24.36	25.52
H. habilis	11.73	10.60	6.98	11.20	7.41	22.72
A. afarensis					20.29	32.83
A. africanus	10.81	7.22	10.55	7.71	8.31	6.16
A. robustus	1.94	6.01	11.06	6.73	15.71	2.73
A. boisei	12.83	19.42	5.36	9.68	13.64	21.66

inion is low on KNM-ER 3733, 3883, and Skull III, intermediate on OH 9, Skull I and II, Pithecanthropus II, and Skull 3, and is high on Sangiran 17 and Pithecanthropus I. KNM-ER 3733 (female) and KNM-ER 3883 (male) both have similar measurements for these characters and Skull III, which has a larger cranial capacity than these African specimens, still has inion positioned low. Thus there is no obvious difference between the African and Asian specimens or between sexes to explain the variability in the position of inion and so these hominids do not follow the same pattern found in pongids (see section 5.4.4 for discussion on the *Pan* vault and sex differences in the position of inion). For V23 (mastoid length) (CV=24.36) KNM-ER 3733, OH 12, Skull II, and Skull 3 (Locus 3) have similar values while KNM-ER 3883 is larger. The value of CV for V24 (mastoid length) is 25.52 and for this measurement KNM-ER 3733, OH 12, Skull II, and Skull 3 (Locus 3) are close in value as are KNM-ER 3883 and OH 9. The other metric traits are less variable.

5.7.5 Face

The values of CV for the face range from 1.36 (F1) to 33.36 (F5 -glabella projection) (see table 5.35). KNM-ER 3733, 3833, and SANGIRAN 17 are close in value for F5 and OH 9 is larger. F15 (simotic chord) (CV=26.84) is similar in KNM-ER 3733 and 3883 but larger in OH 9. The remaining measurements had much lower values of CV.

5.8 Homo habilis

5.8.1 Mandible

The values of CV for the mandible range from 4.65 (M8) to 25.64 (M7) (see table 5.31). For M5 (symphyseal height) (CV=22.73) KNM-ER 1802 (3.7cm) and KNM-ER 1801 (3.2cm) are closer in value than is KNM-ER 1805 (2.32cm). M7 (CV=25.64) is small for SK 45 (1.55cm) but KNM-ER 1805 (2.42cm) and KNM-ER 1802 (2.6cm) have similar values. For M10 (CV=15.19) KNM-ER 1805 (2.7cm) has the lowest and KNM-ER 1803 (4.1cm) the highest values with SK 45 (3.2cm), KNM-ER 1801 (3.3cm), and KNM-ER 1802 (3.55cm) having the closest values. For M12 (CV=12.03) the values of KNM-ER 1801 (6.0cm) and KNM-ER 1805 (6.3cm) are close but that for KNM-ER 1802 is higher (7.5cm). The other traits are less variable.

5.8.2 Palate

The values of CV for the palate range from 6.49 (P2) to 22.31 (P7 -palatal depth at M1) (see table 5.32). For P7 KNM-ER 1470, 1805, 1813, and OH 24 have similar values but STW 53 is much smaller. P9 (bicanine breadth) has a CV of 15.67 where

TABLE 5.35: FOSSIL VALUES OF CV: FACE

SP	F1	F2	F3	F4	F5	F6	
H. erectus	1.37	13.58	3.00	1.66	33.36	2.12	
H. habilis	3.68	26.00	10.61	5.59	31.57	7.74	
A. afarensis							
A. africanus	7.11	8.81	13.66	2.83	20.83	5.95	
A. robustus						2.38	
A. boisei	9.02	26.47	3.34	9.41	26.02	21.92	
	F7	F8	F9	F10	F11	F12	F13
H. erectus	1.92	7.20	12.14	10.86	9.03	7.72	6.20
H. habilis	14.58	7.24	10.59	17.27	11.25	19.24	19.55
A. afarensis							
A. africanus	8.32	9.17	13.23	23.01	15.39	7.63	15.95
A. robustus	11.74		5.04	56.82	8.33	8.85	11.63
A. boisei	10.57	10.19	12.02	116.91	16.35	21.76	20.29
	F14	F15	F16	F17	F18	F19	F20
H. erectus	10.93	26.85		11.03			
H. habilis	5.78	24.81	17.75	11.44	27.56		9.85
A. afarensis							
A. africanus	25.56	58.79	32.11	8.70	3.99	5.07	1.16
A. robustus	11.00	5.11	9.32	5.49	8.46	3.70	0.00
A. boisei	18.26	29.13	26.62	14.18	18.98	5.54	15.98
	F21	F22	F23	F24	F25	F26	F27
H. erectus	6.74	8.22	6.73	5.67	6.27		
H. habilis	16.94	3.32	10.49	11.95	7.28	22.60	
A. afarensis							
A. africanus	13.61		11.44			12.51	21.21
A. robustus	12.60	17.68	0.00	7.31	15.64	21.49	29.18
A. boisei	21.92	2.62	10.63	0.31		0.82	4.83

STW 53 has the lowest value, KNM-ER 1813, OH 24, and SK 847 have intermediate values, and KNM-ER 1470 and 1805 have large values. For P4 (external breadth) (CV=13.06) the values of OH 24 (6.6cm) and KNM-ER 1813 (6.5cm) are again similar with KNM-ER 1805 (8.15cm) larger. The remaining variables have lower values of CV.

5.8.3 Base

Basicranial values of CV range from 1.19 (B21) to 28.1 (B13 -biforamen ovale line-bitympanic line) (see table 5.33). B3 (bitympanic breadth) has a CV of 15.83 where SK 847 (8.6cm) has the lowest value while KNM-ER 1813 (10.25cm) and OH 24 (10.3cm) have similar values with KNM-ER 1805 (11.68cm) and KNM-ER 1470 (13.15cm) having the largest values. For B8 (biforamen ovale breadth) (CV=20.15) KNM-ER 1813 (3.0cm) has the lowest and KNM-ER 1470 (5.4cm) the highest values with KNM-ER 1805 (4.4cm), SK 847 (4.6cm), and OH 24 (4.9cm) in between. For B10 (tympanic-carotid canal) (CV=21.14) KNM-ER 1813 (2.1cm) and SK 847 (2.3cm) are closest in value with higher values for OH 24 (2.95cm), KNM-ER 1805 (3.2cm), and KNM-ER 1470 (3.5cm). For B11 (carotid canal-apex of petrous temporal) (CV=23.35) OH 24 (2.01cm) and SK 847 (2.0cm) have close values but those for KNM-ER 1813 (2.45cm) and KNM-ER 1805 (3.2cm) being higher. OH 24 (4.4cm), 1813 (4.5cm), and SK 847 (4.9cm) have similar values for B12 (biinfratemporal line-bitympanic line) (CV=14.35) as do KNM-ER 1470 (5.7cm) and KNM-ER 1805 (6.05cm). For B13 (CV=28.1) the values of OH 24 (2.3cm), KNM-ER 1813 (2.37cm) and KNM-ER 1470 (2.5cm) are similar and those for SK 847 (3.12cm) and KNM-ER 1805 (4.25cm) are higher. For B14 (biinfratemporal line-basion) (CV=16.43) the values for SK 847 (3.95cm) and OH 24 (4.0cm) are close but those of KNM-ER 1813 (4.45cm), KNM-ER 1470 (4.8cm), and KNM-ER 1805 (5.8cm) are higher. For B15 and B17 only two individuals were measured. For B22 (staphlyon-basion) (CV=24.33) the values range from 3.86 to 6.0 (N=3) and for B24 (post-glenoid process height) (CV=26.09) the values range from .45 to .76cm (N=3). The remaining traits have lower values of CV.

5.8.4 Vault

The values of CV for the vault range from 2.12 (V9) to 31.58 (V11 -inion chord) (see table 5.34). For V7 (CV=26.37) and V8 (21.15) only two individuals were measured. For V11 the values of OH 16 (3.7cm) and KNM-ER 1805 (3.94cm) are similar as are those for KNM-ER 1470 (6.47cm) and KNM-ER 1813 (6.87cm). The same situation occurs for V12 (inion arc) (CV=30.83). For V15 (height of temporal muscle mark) (CV=15.32) the value of KNM-ER 1813 (7.07cm) is low but those for KNM-ER 1805 (9.5cm) and KNM-ER 1470 (9.15cm) are similar. SK 847 (7.9cm) has the lowest value for V17 (biporionic breadth) (CV=17.2) but the values for OH 24 and KNM-ER 1813 (10.2cm), KNM-ER 1805 (11.4cm), and KNM-ER 1470 (12.8cm) are comparable. The values of SK 847 (1.3cm), STW 53 (1.38), and KNM-ER 1805 (1.4cm) are close for V24 (mastoid width) (CV=25.72) but that for KNM-ER 1813 (2.05cm) is higher. The remaining traits have lower values of CV.

5.8.5 Face

The range of values of CV for the face is 3.32 (F22) to 31.57 (F5 -glabella projection) (see table 5.35). For F2 (interorbital breadth) (CV=26.0) SK 847 (1.6cm) and OH 24 (1.77cm) have similar values as do KNM-ER 1813 (2.0cm) and KNM-ER 1470 (2.4cm) but the value for KNM-ER 1805 (3.0cm) is higher. For F5 the values range from .5 to 1.2cm (N=5). OH 24 (1.25cm) and SK 847 (2.0) have the lowest and highest values for F10 (zygomaxillary subtense) (CV=17.27) with the values of KNM-ER 1470 (1.5cm), KNM-ER 1813 (1.6cm), and KNM-ER 1805 (1.75) being similar. For F12 (upper facial height) (CV=19.24) only KNM-ER 1813 and STW 53 are close in value, the other specimens being smaller or larger for this variable. For F13 (nasal height) (CV=19.55), KNM-ER 1813, OH 24, and STW 53 are closest in value with SK 847, KNM-ER 1805 and 1470 having larger values. For F16 (CV=17.75) there is no clustering of values. The values of KNM-ER 1805 (.43cm) and KNM-ER 1813 (.38cm) are close for F15 (simotic chord) (CV=24.81) as are those for KNM-ER 1470 (.62cm) and OH 24 (.7cm) with STW 53 intermediate in value. For F18 (CV=27.56) and F26 (CV=22.6) only two individuals were measured. For F21 (minimum cheek height) (CV=16.94) KNM-ER 1813 (2.7cm), STW 53 (2.95cm), OH 24 (3.0cm), SK 847 (3.03cm), and 1805 (3.31cm) are closer in value than is KNM-ER 1470 (4.24cm). The remaining traits have lower values of CV.

5.9 A. afarensis

5.9.1 Mandible

The range of values of CV for the mandible is 10.16 (M12) to 47.60 (M4 - minimum ramus breadth) (see table 5.31). For M1 (bigonial breadth) (CV=15.79) A. L. 288.1 (7.0cm), A. L. 400.1 (8.25cm), and LH 4 (8.5cm) form one group with low values and A. L. 311.1 (9.6cm), A. L. 207.13 (10.0cm), A. L. 198.1 (11.0cm) and A. L. 333w.60 (11.4cm) have higher values. M3 (length) (CV=32.49), M4, and M6 (coronoid height) (CV=32.7) were only measured on two individuals (A. L. 288.1 and Reconstruction) and they are presumably female and male individuals. The remaining variables have lower values of CV.

5.9.2 Palate

The values of CV for the palate range from 5.69 (P4) to 21.17 (P9 -bicanine breadth) (see table 5.32). For P1 (CV=18.86) and P5 (CV=20.51) only two individuals were measured. P7 (CV=17.29) is a small measurement and there is no clustering of values. For P9 the variability is caused by A. L. 200.1 which has a larger value than A. L. 199.1 and A. L. 333.2. In all the palatal variables measured A. L. 200.1 had larger values than A. L. 199.1. The rest of the variables had lower values of CV.

5.9.3 Base

Only four measurements were taken in this region (B16, B20, B23, B24) (see table 5.33). For B16 (CV=14.46), B23 (CV=47.14), and B24 (CV=23.57) only two individuals were measured and B20 (CV=3.82) is not variable although only two individuals were measured.

5.9.4 Vault

The values of CV for the vault range from 1.1 (V11) to 32.83 (V24) but only five variables were measured (V2, V11, V12, V23, V24) and the measurements of only two individuals per variable were obtained (see table 5.34).

5.9.5 Face

Measurements of the face of A. afarensis were only obtained from the reconstructed cranium.

5.10 A. africanus

5.10.1 Mandible

The range of values of CV for the mandible is 2.81 (M1) to 20.89 (M8 -internal breadth) (see table 5.31). For M2 (foramen mentalia breadth) (CV=14.07) there is not a great difference between, and no clustering of, values. For M5 (symphyseal height) (CV=14.51) STS 52, STS 36, and MLD 40 have similar values and STS 7 is larger. For M8 STS 36 and STS 52 have close values and MLD 18 is much smaller. The remaining variables have lower values of CV.

5.10.2 Palate

The values of CV for the palate range from 6.19 (P3) to 34.0 (P8 -palatal depth at M3) (see table 5.32). For P2 (internal breadth) (CV=17.89) MLD 6 (2.6cm) and STS 52 (2.6cm) have the same values, STS 53 (3.67cm) and STS 5 (3.6cm) are close in value, and STW 73 is intermediate between the two groups. For P7 (palatal depth at M1) (CV=28.40) some individuals have lower values (STW 391, STS 71, STS 53), some intermediate values (STW 73, MLD 6, MLD 9), and some higher values (STW 13, STW 252, STS 5, STS 17, STS 52, TM 1511). For P8 STW 73 (1.65cm) has the largest value, STS 53 (.65cm) the lowest value, and STS 5 (1.35cm) and TM 1511 (1.30) are intermediate between the two. The values of CV for the remaining characters are lower.

5.10.3 Base

The values of CV for the base range from 1.53 (B4) to 30.75 (B7-bipetrous width) (see table 5.33). For B7 STS 25 has a smaller value than MLD 37/38, STS 19, and STS 5. For B13 (biforamen ovale line-bitympanic line) (CV=22.27) STS 25 has a higher value than the other specimens and may have been incorrectly measured (see Chapter 6, section 6.2.3, for discussion). For B14 (biinfratemporal line-basion) (CV=11.23) STS 19 has the lowest value, STS 25 the highest value, while those of STS 5 and MLD 37/38 are intermediate. For B21 (sphenooccipital synchrondosis-staphlyon chord) (CV=12.22) MLD 37/38 and STS 5 are closer in value than STS 19 which has a higher value. For B23 (articular eminence height) (CV=27.7) STS 5 has the lowest value (.4cm), MLD 37/38 (.65cm), STS 71 (.60cm), and STS 19 (.7cm) have intermediate values, and TM 1511 has the highest value (.9cm). For B24 (CV=29.86) MLD 37/38 (.7cm), STS 5 (.65cm), TM 1511 (.6cm) and STS 25 (.50cm) are closer in value than is STS 19 (1.05cm) which is larger. The remaining variables have lower values of CV.

5.10.4 Vault

Values of CV range from 1.52 (V16) to 44.54 (V13- nuchal chord) in this region (see table 5.34). For V1 (frontal breadth) (CV=17.19) and V10 (supraglabellare-bregma) (CV=21.21) only two individuals (STS 5 and STS 71) were measured. For V11 (inion chord) (CV=22.49) MLD 37/38 has the lowest value (4.07cm), STS 71 the highest (6.6cm) and MLD 1 (4.55cm) and STS 5 (4.65cm) are close in value. For V13 there is a wide range of values from .9cm to 3.24cm. For V14 (nuchal arc) (CV=44.20) STS 26 (1.0cm) has the lowest value, MLD 37/38 (2.5cm) and MLD 1 (3.3cm) the highest values, and STS 5 (1.6cm) and STS 71 (1.7cm) are closest in value. The remaining traits have lower values of CV.

5.10.5 Face

The values of CV for the face range from 1.16 (F20) to 58.79 (F15 -simotic chord) (see table 5.35). For F5 (glabella projection) (CV=20.83) and F15 there is no clustering of values though the range of values is small. For F10 (zygomaxillary subtense) (CV=23.01), STS 52 has the largest value (2.25cm), STS 5 the lowest value (1.2cm), and the remaining specimens have intermediate values. For F9 (bimaxillary chord) (CV=13.23) STS 17 (7.4cm) and TM 1511 have estimated values and STS 52 (9.1cm), STS 71 (9.4cm) and STS 5 (10.6cm) are close in value. For F11 (subspinale-zygomaxillare chord) (CV=15.39) STS 71 (4.93cm) and STS 52 (5.0cm) have the closest values with STS 17 (4.1cm) and TM 1511 (4.28cm) having the lowest and STS 5 (6.0cm) the highest values. For F13 (nasal height) (CV=15.95) STS 63 has the largest value (7.17cm) then STW 13 (5.7cm), with STS 5 (4.9cm), STS 17 (5.0cm), STS 71 (5.34cm), STS 52 (4.96cm), TM 1511 (4.65cm), and MLD 6 (4.57cm) having the closest values. All of the values for F14 (nasal breadth) (CV=25.56) range from 2.25 to 2.90cm except MLD 9 (3.9cm) and TM 1511 (4.8cm) (N=11). STS 5 (1.7cm) and STW 13 (1.27cm) have higher values for F16 (zygomatic root-alveolar margin) (CV=32.11) than STS 53 (.84cm), STS 17 (.63cm), STS 71 (.87cm), TM 1511 (.87cm), STS 52 (.82cm), MLD 9 (.93cm), and MLD 6 (.93cm) which are closer in value. For F27 (zygomatic arch thickness) (CV=21.21) only two individuals were measured. The remaining traits have lower values of CV.

5.11 A. robustus

5.11.1 Mandible

The values of CV of the mandible range from 5.66 (M3) to 19.43 (M11- depth at M3) (see table 5.31). For M11 SK 12 and SK 844 have similar values and SK 23 is larger. For M10 (depth at M1) (CV=11.4) SK 12 and SK 876 are more similar as are SK 23, SK 34, and TM 1517. The remaining values of CV are lower.

5.11.2 Palate

Values of CV range from 3.6 (P5) to 31.6 (P8 -depth at M3) (see table 5.32). For P8 and P7 (depth at M1) (CV=18.0) TM 1517 has the lowest value and the remaining values cluster together. For P1 (length) (CV=11.4) and P9 bicanine breadth (CV=15.32) there is no clustering of values. The other characters have lower values of CV.

5.11.3 Base

Only four measurements were taken in this region (B21 - 24) (see table 5.33). B21 (sphenooccipital synchrondosis-staphlyon chord) (CV=11.06) and B22 (staphlyon-basion chord) (CV=28.22) were only measured on two individuals. B23 (articular eminence height) (CV=19.55) and B24 (post-glenoid process height) (CV=47.5) are small measurements so the differences between values are magnified since both these measurements have a small range of values.

5.11.4 Vault

Only seven measurements were taken in the vault region and the values of CV range from 1.94 (V17, V19) to 35.0 (V10 -supraglabellare-bregma) (see table 5.34). For V10 only two individuals were measured. V17 (biporionic breadth), V19 (porion-zygoorbitale), V20 (porion-zygomaxillare) and V22 (biauricular breadth) have low values of CV but it is interesting to note that the same two individuals, SK 48 and TM 1517, have similar values for these measurements. For V23 (mastoid length) (CV=15.71) only SK 26 (2.4cm) and SK 83 (3.0cm) were measured as well as for V24 (mastoid width) for which there is a lower value of CV since the measurements are closer in value.

5.11.5 Face

The values of CV for the face range from 0.0 (F20, F23) to 56.82 (F10- zygo-maxillary subtense) (see table 5.35). For F10 SK 48 and SK 12 have close values but SK 46 is larger. For F22 (superior facial height) (CV=17.68) and F25 basi-alveolar length) (CV=15.64) SK 48 (9.8cm, 9.55cm) has smaller values than SK 83 (12.6cm, 12.3cm). For F26 (zygomatic arch depth) (CV=21.49) SK 48 (1.63cm) has a larger value than TM 1517 (1.2cm) but for F27 (zygomatic arch thickness) (CV=29.18) the opposite is true. The remaining traits have lower values of CV.

5.12 A. boisei

5.12.1 Mandible

For *A. boisei* the values of CV for the mandible range from 4.90 (M4) to 23.11 (M6 -coronoid height) (see table 5.31). For M6 only two individuals were measured. The remaining variables have much lower values of CV.

5.12.2 Palate

The values of CV for the palate range from 1.88 (P4) to 19.87 (P8 -palatal depth at M3) (see table 5.32). For P7 (palatal depth at M1) (CV=15.29) the value for KNM-ER 3891 is less than for the other individuals. For P8 OH 5 and KNM-ER 406 are closer in value than KNM-ER 405 which is slightly larger. The values for P9 (bicanine breadth) are all close (CV=15.67) but KNM-ER 403 and KNM-ER 3899 are closest in value. The remaining characters are less variable.

5.12.3 Base

The values of CV range from 1.57 (B21) to 43.04 (B23 -articular eminence height) for the base (see table 5.33). OH 5 and KNM-ER 406 are closest in value for B6 (bicarotid canal width) (CV=24.34) with smaller values for KNM-ER 732 and KNM-ER 407. For B7 (bipetrous width) (CV=31.11) OH 5 and KNM-ER 407 have similar values and those for KNM-ER 406 and KNM-ER 732 are less. For B8 (biforamen ovale width) (CV=16.84) KNM-ER 407 and KNM-ER 732 have similar values as do KNM-ER 406 and OH 5. KNM-ER 407 is the smallest for B10 (tympanic-carotid canal) (CV=15.03) but KNM-ER 406, KNM-ER 732, and OH 5 are of similar size. For B11 (carotid canal-apex petrous temporal) (CV=20.11) KNM-ER 732 is the smallest, KNM-ER 406 the largest, and KNM-ER 407 and OH 5 have the closest values. For B14 (biinfratemporal line-basion) (CV=16.83) OH 5 and KNM-ER 406 have similar values and KNM-ER 407 is smaller in size. OH 5 and KNM-ER 406 have similar values for B17 (breadth across supramastoid crests) (CV=14.62) as do KNM-ER 407 and KNM-ER 732. B18 (CV=21.79) is similar for KNM-ER 406, KNM-ER 407, and OH 5 but the value for KNM-ER 732 is lower. KNM-ER 407 has the smallest value for B20 (lateral nuchal crest arc) (CV=17.79) but the values of KNM-ER 406 and OH 5 are similar. B23 and B24 are highly variable characters due to the fact they are such small measurements that differences in values are magnified. The other variables in this region are less variable.

5.12.4 Vault

The values of CV for the vault (see table 5.34) range from 3.19 (V1) to 30.43 (V10 -supraglabellare - bregma). For V3 (frontal arc), F4 (frontal chord), V10, V15 (height of temporal muscle mark), V19 (porion - zygoorbitale), and V20 (porion - zygomaxillare) OH 5 and KNM-ER 406 are close in value and that of KNM-ER 732 is much less. For V16 (temporal muscle mark arc) (CV=14.76) OH 5 has the largest value, followed by KNM-ER 406, and then KNM-ER 732. For V23 and V24 (mastoid length and width) OH 5 and KNM-ER 406 have similar values as do KNM-ER 407 and KNM-ER 732. The rest of the characters of the vault are less variable.

5.12.5 Face

The values of CV for the face range from 0.31 (V24) to 116.91 (F10) (see table 5.35). For F10 KNM-ER 406 (1.1cm) and KNM-ER 732 (0.5cm) are closer in value than is OH 5 (5.7cm). The reason for the large difference in values is due to the nature of the measurement. F10 (zygomaxillary subtense) is the distance subtended by subspinale (SS) from the line ZM/ZM (zygomaxillare). If the individual is not prognathic and the cheek region not prominent the measurement will be small. The measurement will also be small if the individual is prognathic and has prominent cheek bones. However, if the individual is prognathic but without prominent cheek bones (or anteriorly situated ZM) then the measurement can be large. Thus the nature of the measurement allows such great variability in values.

For the measurements F2 (interorbital breadth), F5 (glabella projection), F6 (bizygomatic breadth at orbits), F11 (subspinale-zygomaxillare), F17 (bizygomatic tubercle breadth), and F21 (cheek height) OH 5 and KNM-ER 406 have similar values and KNM-ER 732 is smaller in size. For F12 (upper facial height) and F13 (nasal height) OH 5 has the largest values followed by KNM-ER 406, then KNM-ER 732. For F14 (nasal breadth) OH 5 and KNM-ER 405 are closer in value than KNM-ER 406 and KNM-ER 732. F15 and F16 are small measurements with the values of F15 being spread out but for F16 KNM-ER 406 and KNM-ER 732 are close in value as are KNM-ER 405 and OH 5. For F18 (superior malar length) and F19 (inferior malar length) only KNM-ER 406 and OH 5 were measured with OH 5 the largest for both variables. The remaining characters are less variable.

5.13 Overall Effect On Fossil Crania

The fossil specimens seem to be showing variability in the same areas as in the modern groups. Differences in mandibular and palatal measurements seem to be due to size. In the base, width measurements vary as does the area (length and width) of the basicranial axis region and both the temporal and nuchal muscle areas show variability. The face varies in size (length, height, and width) and in the amount of prognathism. The sample statistics of the fossil hominids can be found in tables 5.36-5.65.

H. erectus shows some overlap in size between the African and Asian specimens. With *H. habilis* KNM-ER 1470 and 1805 possess a number of measurements in common in which they are both larger than the other specimens. Most of the information concerning *A. afarensis* was derived from the mandible and palate regions where in the mandible, A. L. 288.1 (female) is the smallest and A. L. 333w.60 is presumed to be a male and in the palate, A. L. 200.1 is larger in all measurements than A. L. 199.1. Of the *A. africanus* specimens, STS 5, STS 71, and MLD 37/38 are similar in size for a number of measurements but there is no discernable pattern of size difference in this group. Of the *A. robustus* specimens, SK 48 and TM 1517 share similar values in the vault region. Within *A. boisei* KNM-ER 406 and OH 5 consistently grouped together as did KNM-ER 732 and 407.

TABLE 5.36: H.ERECTUS: SUMMARY STATISTICS: MANDIBLE

VAR.	NO.	MEAN	STDDEV
M1	7	9.681	.740
M2	7	4.963	.948
M3	7	11.729	.844
M4	5	4.776	.615
M5	13	3.118	.367
M6	5	7.424	.381
M7	12	2.197	.261
M8	7	4.984	.717
M9	7	7.057	.484
M10	15	2.941	.360
M11	11	2.982	.347
M12	10	5.930	.386

TABLE 5.37: H. HABILIS: SUMMARY STATISTICS: MANDIBLE

VAR.	NO.	MEAN	STDDEV
M1	1	9.000	
M2	2	4.570	.325
M5	3	3.073	.699
M7	3	2.190	.562
M8	2	4.260	.198
M9	2	6.855	.431
M10	5	3.370	.512
M11	3	3.017	.161
M12	3	6.600	.794

TABLE 5.38: A. AFARENSIS:SUMMARY STATISTICS: MANDIBLE

VAR.	NO.	MEAN	STDDEV
M1	7	9.393	1.573
M2	11	4.408	.433
M3	2	11.425	3.712
M4	2	4.145	1.973
M5	11	3.414	.463
M6	2	7.415	2.425
M7	13	2.343	.274
M8	7	4.086	.567
M9	7	7.114	.944
M10	12	3.196	.324
M11	8	2.850	.396
M12	12	6.462	.601

TABLE 5.39: A. AFRICANUS:SUMMARY STATISTICS: MANDIBLE

VAR.	NO.	MEAN	STDDEV
M1	4	8.950	.252
M2	5	4.780	.672
M3	3	11.433	.666
M4	3	4.747	.435
M5	4	3.462	.502
M6	3	7.003	.443
M7	13	2.528	.262
M8	3	5.140	1.074
M9	3	7.343	.679
M10	9	3.217	.341
M11	7	2.857	.249
M12	6	6.750	.327

TABLE 5.40: A. ROBUSTUS: SUMMARY STATISTICS: MANDIBLE

VAR.	NO.	MEAN	STDDEV
M1	1	13.700	
M2	1	5.200	
M3	3	13.733	.777
M4	5	5.254	.527
M5	2	4.525	.389
M6	3	9.807	.690
M7	4	3.147	.282
M8	1	6.420	
M9	1	8.470	
M10	5	3.860	.373
M11	6	3.583	.696
M12	3	7.300	.781

TABLE 5.41: A. BOISEI: SUMMARY STATISTICS: MANDIBLE

VAR.	NO.	MEAN	STDDEV
M1	3	11.473	1.434
M2	3	5.390	.537
M3	2	13.700	1.131
M4	2	5.490	.269
M5	5	4.710	.361
M6	2	9.0250	2.086
M7	17	3.422	.378
M8	3	6.277	.712
M9	3	8.773	.863
M10	21	4.049	.395
M11	17	3.850	.504
M12	13	7.966	.592

TABLE 5.42: H. ERECTUS: SUMMARY STATISTICS: PALATE

VAR.	NO.	MEAN	STDDEV
P1	2	4.900	.141
P2	1	4.800	
P3	2	6.800	.566
P4	1	8.070	
P5	1	5.800	
P6	1	7.350	
P7	3	1.217	.491
P8	3	1.353	.605
P9	2	3.325	.035

TABLE 5.43: H. HABILIS: SUMMARY STATISTICS: PALATE

VAR.	NO.	MEAN	STDDEV
P1	5	5.414	.474
P2	3	3.467	.225
P3	5	6.548	.591
P4	3	7.083	.925
P5	4	6.532	.606
P6	4	6.822	.668
P7	5	1.210	.270
P8	3	1.143	.098
P9	6	2.930	.459

TABLE 5.44: A. AFARENSIS: SUMMARY STATISTICS: PALATE

VAR.	NO.	MEAN	STDDEV
P1	2	6.000	1.131
P2	2	3.250	.354
P3	2	6.600	.707
P4	2	6.460	.368
P5	2	6.550	1.344
P6	2	6.065	.375
P7	3	.883	.153
P8	1	1.100	
P9	3	2.530	.536

TABLE 5.45: A. AFRICANUS: SUMMARY STATISTICS: PALATE

VAR.	NO.	MEAN	STDDEV
P1	6	5.922	.548
P2	6	3.270	.585
P3	5	6.854	.424
P4	6	6.163	.620
P5	4	6.705	.431
P6	4	5.980	.755
P7	12	1.250	.355
P8	4	1.237	.421
P9	12	2.789	.333

TABLE 5.46: A. ROBUSTUS: SUMMARY STATISTICS: PALATE

VAR.	NO.	MEAN	STDDEV
P1	5	5.958	.680
P2	4	3.967	.365
P3	5	7.248	.423
P4	4	7.302	.486
P5	4	6.377	.230
P6	5	7.080	.520
P7	8	1.342	.241
P8	5	1.612	.509
P9	8	2.604	.390

TABLE 5.47: A. BOISEI: SUMMARY STATISTICS: PALATE

VAR.	NO.	MEAN	STDDEV
P1	3	7.050	.634
P2	3	3.833	.230
P3	3	8.047	.388
P4	3	7.980	.150
P5	3	7.147	.771
P6	2	8.005	.474
P7	5	1.716	.262
P8	3	1.767	.351
P9	4	2.612	.409

TABLE 5.48: H. ERECTUS: SUMMARY STATISTICS: BASE

VAR.	NO.	MEAN	STDDEV
B1	3	3.553	.452
B2	3	2.983	.333
B3	9	12.253	.585
B4	4	9.045	.562
B5	4	8.287	.649
B6	4	6.100	.474
B7	4	3.787	1.096
B8	4	5.782	.309
B9	4	7.637	1.277
B10	4	2.837	.165
B11	4	2.490	.202
B12	4	5.725	.275
B13	4	2.845	.308
B14	4	5.550	.332
B15	4	2.720	.293
B16	11	11.233	.682
B17	9	14.243	.766
B18	7	10.929	.770
B19	9	6.392	.689
B20	10	8.890	1.978
B21	1	4.620	
B22	1	6.500	
B23	3	1.183	.621
B24	3	.500	.132

TABLE 5.49: H. HABILIS: SUMMARY STATISTICS: BASE

VAR.	NO.	MEAN	STDDEV
B1	2	2.990	.127
B2	2	2.525	.106
B3	5	10.796	1.709
B4	4	7.090	.501
B5	4	6.612	.501
B6	5	5.070	.659
B7	4	2.160	.145
B8	5	4.460	.899
B9	5	6.138	.748
B10	5	2.810	.594
B11	4	2.415	.564
B12	5	5.110	.733
B13	5	2.908	.817
B14	5	4.600	.756
B15	2	1.805	.276
B16	4	9.400	.729
B17	2	12.240	1.499
B18	3	9.453	.705
B19	3	5.520	.330
B20	3	6.933	.404
B21	2	2.975	.035
B22	3	4.703	1.140
B23	4	.662	.048
B24	4	.662	.137

TABLE 5.50: A. AFARENSIS: SUMMARY STATISTICS: BASE

VAR.	NO.	MEAN	STDDEV
B1	1	2.900	
B3	1	12.600	
B4	1	8.000	
B5	1	6.800	
B6	1	5.600	
B7	1	3.000	
B8	1	4.600	
B10	1	3.150	
B11	1	3.000	
B13	1	3.000	
B16	2	8.800	1.273
B17	1	12.700	
B18	1	10.000	
B19	1	4.800	
B20	2	5.550	.212
B23	2	.225	.106
B24	2	.600	.141

TABLE 5.51: A. AFRICANUS: SUMMARY STATISTICS: BASE

VAR.	NO.	MEAN	STDDEV
B1	4	2.805	.137
B2	4	2.367	.276
B3	4	9.262	.304
B4	3	6.817	.104
B5	3	6.357	.214
B6	4	4.655	.360
B7	4	2.182	.671
B8	4	4.427	.322
B9	4	4.875	.222
B10	4	2.375	.096
B11	4	2.375	.206
B12	4	4.812	.551
B13	4	2.775	.618
B14	4	4.487	.504
B15	3	2.240	.242
B16	4	7.675	.359
B17	4	11.290	.698
B18	4	8.875	.450
B19	2	5.300	.283
B20	2	6.150	.495
B21	3	3.867	.473
B22	3	5.373	.155
B23	5	.650	.180
B24	5	.700	.209

TABLE 5.52: A. ROBUSTUS: SUMMARY STATISTICS: BASE

VAR.	NO.	MEAN	STDDEV
B1	1	2.640	
B2	1	2.420	
B3	1	11.800	
B4	1	6.700	
B5	1	6.600	
B6	1	4.800	
B7	1	1.900	
B8	1	4.200	
B9	1	6.100	
B10	1	3.400	
B11	1	2.200	
B12	1	6.200	
B13	1	3.400	
B14	1	5.700	
B15	1	2.300	
B17	1	12.800	
B18	1	11.00	
B21	2	3.580	.396
B22	2	4.585	1.294
B23	4	.532	.104
B24	4	.737	.350

TABLE 5.53: A. BOISEI: SUMMARY STATISTICS: BASE

VAR.	NO.	MEAN	STDDEV
B1	3	2.873	.064
B2	3	2.900	.310
B3	4	11.580	1.380
B4	3	7.967	.611
B5	3	7.207	.716
B6	4	5.302	1.291
B7	4	2.275	.708
B8	4	5.030	.847
B9	4	6.190	.208
B10	4	3.260	.490
B11	4	2.335	.470
B12	4	5.280	.584
B13	4	3.237	.229
B14	3	4.883	.822
B15	3	2.660	.362
B16	3	9.090	.906
B17	4	11.767	1.721
B18	4	11.240	2.449
B19	3	5.093	.490
B20	3	6.267	1.115
B21	2	4.055	.064
B22	2	6.025	.148
B23	4	.942	.406
B24	4	.862	.328

TABLE 5.54: H. ERECTUS: SUMMARY STATISTICS: VAULT

VAR.	NO.	MEAN	STDDEV
V1	10	10.422	.598
V2	10	13.350	.459
V3	9	12.644	.721
V4	10	10.437	.937
V5	10	10.430	1.699
V6	10	9.743	1.562
V7	10	11.180	1.313
V8	10	7.925	.799
V9	8	10.894	.404
V10	10	8.056	1.020
V11	12	5.075	1.011
V12	12	5.529	1.332
V13	10	5.113	1.357
V14	10	5.780	1.711
V15	3	8.650	.328
V16	3	25.167	2.566
V17	9	12.742	.687
V18	4	10.575	.318
V19	3	8.950	.606
V20	3	8.117	.769
V21	10	18.285	1.076
V22	7	13.221	.797
V23	5	2.040	.599
V24	6	1.983	.506

TABLE 5.55: H. HABILIS: SUMMARY STATISTICS: VAULT

VAR.	NO.	MEAN	STDDEV
V1	6	8.883	.765
V2	6	10.642	.819
V3	5	9.690	.445
V4	5	8.334	.628
V5	6	8.600	1.020
V6	6	7.995	.875
V7	2	8.850	2.333
V8	2	7.290	1.541
V9	3	8.917	.189
V10	6	6.422	.373
V11	4	5.245	1.656
V12	4	5.725	1.765
V13	1	3.150	
V14	1	3.100	
V15	3	8.573	1.314
V16	3	22.833	3.014
V17	5	10.500	1.806
V18	4	8.755	1.011
V19	4	8.267	.970
V20	4	7.807	.828
V21	5	14.740	1.029
V22	4	11.600	1.299
V23	4	2.375	.176
V24	4	1.532	.348

TABLE 5.56: A. AFARENSIS: SUMMARY STATISTICS: VAULT

VAR.	NO.	MEAN	STDDEV
V2	2	9.150	.778
V7	1	7.300	
V8	1	6.100	
V11	2	3.225	.035
V12	2	3.350	.071
V13	1	3.920	
V14	1	4.000	
V17	1	12.000	
V23	2	2.335	.474
V24	2	2.800	.919

TABLE 5.57: A. AFRICANUS: SUMMARY STATISTICS: VAULT

VAR.	NO.	MEAN	STDDEV
V1	2	7.550	1.344
V2	3	9.333	.814
V3	2	8.700	.141
V4	2	7.350	.212
V5	6	8.417	.387
V6	6	7.662	.467
V7	4	7.375	.330
V8	4	6.162	.439
V9	2	9.775	.742
V10	2	6.000	1.273
V11	4	4.967	1.117
V12	4	5.275	.613
V13	5	2.016	.898
V14	5	2.020	.893
V15	2	7.975	.177
V16	2	23.250	.354
V17	4	9.025	1.008
V18	2	8.380	.877
V19	2	8.175	.884
V20	2	7.840	.566
V21	2	13.400	1.414
V22	4	10.100	.779
V23	3	2.143	.178
V24	3	1.867	.115

TABLE 5.58: A. ROBUSTUS: SUMMARY STATISTICS: VAULT

VAR.	NO.	MEAN	STDDEV
V1	1	8.230	
V3	1	6.300	
V4	1	6.030	
V10	2	2.950	1.032
V17	2	10.950	.212
V18	1	9.250	
V19	2	9.125	.177
V20	2	9.880	.594
V21	1	13.500	
V22	2	11.550	.778
V23	2	2.700	.424
V24	2	2.590	.071

TABLE 5.59: A. BOISEI: SUMMARY STATISTICS: VAULT

VAR.	NO.	MEAN	STDDEV
V1	4	8.325	.265
V2	4	9.500	.707
V3	3	9.133	1.935
V4	3	8.253	1.873
V5	3	9.867	.603
V6	3	8.977	.391
V7	3	7.500	.361
V8	3	6.017	.222
V9	2	10.000	.919
V10	3	5.250	1.598
V11	4	3.812	.208
V12	4	4.100	.216
V13	3	3.233	.344
V14	3	3.333	.404
V15	3	9.440	1.316
V16	3	27.167	4.010
V17	4	11.850	1.287
V18	3	10.097	.908
V19	3	9.623	1.235
V20	3	10.347	2.009
V21	2	16.475	.884
V22	4	12.607	1.220
V23	4	2.855	.389
V24	4	2.765	.599

TABLE 5.60: H. ERECTUS: SUMMARY STATISTICS: FACE

VAR.	NO.	MEAN	STDDEV
F1	3	10.763	.148
F2	4	2.525	.343
F3	3	4.547	.136
F4	3	3.620	.060
F5	4	1.307	.436
F6	3	12.377	.261
F7	3	13.800	.265
F8	4	11.375	.819
F9	2	10.880	1.386
F10	2	2.275	.247
F11	2	6.110	.552
F12	2	7.510	.580
F13	3	5.327	.330
F14	3	3.230	.353
F15	3	.803	.216
F16	1	1.000	
F17	2	10.520	1.160
F18	1	4.410	
F19	1	4.700	
F20	1	3.600	
F21	2	3.455	.233
F22	2	12.475	1.025
F23	4	8.310	.559
F24	4	10.687	.606
F25	2	12.295	.771
F26	1	1.150	
F27	1	.400	

TABLE 5.61: H. HABILIS: SUMMARY STATISTICS: FACE

VAR.	NO.	MEAN	STDDEV
F1	5	9.352	.344
F2	5	2.154	.560
F3	5	3.736	.396
F4	5	3.192	.179
F5	5	.820	.259
F6	5	10.500	.812
F7	3	11.900	1.735
F8	6	9.543	.691
F9	5	9.900	1.049
F10	5	1.620	.280
F11	5	5.202	.585
F12	6	6.955	1.338
F13	6	4.618	.903
F14	5	2.576	.149
F15	5	.532	.132
F16	5	1.034	.184
F17	4	10.125	1.159
F18	2	3.130	.863
F19	1	4.450	
F20	2	4.020	.396
F21	6	3.205	.543
F22	2	9.165	.304
F23	4	7.352	.771
F24	2	7.100	.849
F25	3	8.977	.654
F26	2	1.095	.247
F27	1	.360	

TABLE 5.62: A. AFARENSIS: SUMMARY STATISTICS: FACE

VAR.	NO.	MEAN	STDDEV
F14	1	2.080	
F16	1	.910	

TABLE 5.63: A. AFRICANUS: SUMMARY STATISTICS: FACE

VAR.	NO.	MEAN	STDDEV
F1	5	7.980	.567
F2	6	1.770	.156
F3	5	3.244	.443
F4	4	3.057	.087
F5	3	.733	.153
F6	4	10.685	.636
F7	2	11.900	.990
F8	4	8.342	.765
F9	5	8.980	1.188
F10	5	1.730	.398
F11	5	4.862	.748
F12	6	6.833	.521
F13	8	5.286	.843
F14	11	2.930	.749
F15	4	.347	.204
F16	9	.984	.316
F17	3	9.367	.814
F18	2	4.425	.177
F19	2	5.020	.255
F20	2	3.670	.042
F21	7	2.814	.383
F22	1	12.400	
F23	2	7.725	.884
F24	1	9.800	
F25	1	12.400	
F26	2	.735	.092
F27	2	.400	.085

TABLE 5.64: A. ROBUSTUS: SUMMARY STATISTICS: FACE

VAR.	NO.	MEAN	STDDEV
F1	1	10.100	
F2	1	2.500	
F3	1	3.600	
F4	1	3.000	
F5	1	1.250	
F6	2	11.900	.283
F7	2	13.850	1.626
F8	1	9.800	
F9	3	10.883	.548
F10	3	.667	.379
F11	3	5.500	.458
F12	2	7.190	.636
F13	3	5.073	.590
F14	6	2.760	.303
F15	2	.415	.021
F16	8	1.169	.109
F17	2	10.300	.566
F18	2	4.680	.396
F19	2	5.730	.212
F20	2	5.250	.000
F21	4	3.170	.399
F22	2	11.200	1.980
F23	2	8.300	.000
F24	2	8.225	.601
F25	2	11.075	1.732
F26	2	1.415	.304
F27	2	.630	.184

TABLE 5.65: A. BOISEI: SUMMARY STATISTICS: FACE

VAR.	NO.	MEAN	STDDEV
F1	2	10.745	.205
F2	3	2.427	.345
F3	2	4.570	.184
F4	2	3.590	.042
F5	3	1.410	.471
F6	2	12.240	.156
F7	2	13.750	.354
F8	3	11.533	.925
F9	2	11.850	2.758
F10	1	2.100	
F11	1	5.720	
F12	1	7.920	
F13	2	5.490	.240
F14	2	3.365	.375
F15	3	.803	.216
F16	1	1.000	
F17	1	9.700	
F18	2	4.905	.700
F19	2	5.450	1.061
F20	2	3.400	.283
F21	2	3.570	.396
F22	1	11.750	
F23	3	8.340	.681
F24	3	10.650	.737
F25	1	11.750	
F26	1	1.150	
F27	1	.400	

UNIVARIATE ANALYSIS 2: BETWEEN SPECIES VARIATION

5.14 Introduction

The purpose of examining between species variation of the modern groups is to determine a) if any common pattern of primate sexual dimorphism exists which could be used to assess fossil hominid sexual dimorphism; and b) if characters exist which would be useful in discriminating between species in order to address the first two aims of this thesis.

5.15 Mandible

5.15.1 Variance

For both *Pan* and *Gorilla* the variance is significant for M4 (ramus breadth) and for *Pan* and *Pongo*, M8 (internal breadth) (see table 5.01, 5.16, 5.21, 5.26).

The range of CV at the species level (4 species combined sexes) and of the sexes were examined to determine if any pattern existed. For example, for M1 the species values for CV range from 10.34 (PA) to 14.04 (PO), male values range from 7.51 (PA) to 13.11 (PO), and female values range from 7.04 (PO) to 11.13 (PA). The ranges of males and females overlap considerably for M1 but for *Pan* the female value of CV is 1.5 times greater than the male value and for *Pongo* the male value is 1.7 times greater than the female value. The within-species values for the sexes of *H. sapiens* and *Gorilla* are similar for this variable (see table 5.02).

The ranges of the values of CV for the sexes greatly overlap for all variables but M4. There is a significant difference in variance for M4 in *Pan* and *Gorilla* and a significant difference in the means in all species. The species values range from 9.24 (HS) to 17.15 (GO), the male values from 7.83 (HS) to 11.23 (PO), and the female values from 5.06 (PA) to 8.35 (HS). Thus the ranges of the sexes overlap somewhat with males having generally higher values than females.

An examination of the breakdown of mean values of CV for the mandible (see table 5.66) shows that the values are very similar for all four species with male values greater than female values for *H. sapiens*, *Pan*, *Gorilla*, and *Pongo.*

5.15.2 Means

The four species share 5 variables where the means are significant (M1, M3 - 6). *H. sapiens*, *Gorilla*, and *Pongo* share 4 variables (M2, M9 - 11) and *Gorilla* and *Pongo* one variable (M12) (see table 5.01, 5.16, 5.21, 5.26).

Looking at Table 5.67, the mean values for percentage sexual dimorphism, the

TABLE 5.66: HOMINOIDS: BREAKDOWN OF MEAN CV

Sp	Sex	Mandible	Palate	Base	Vault	Face	Total Mean
HS	M	8.66	10.35	9.33	6.97	8.92	8.64
	F	7.49	8.67	10.64	8.37	10.47	9.13
PA	M	7.30	7.46	10.83	10.52	10.22	9.27
	F	7.23	9.03	9.82	11.94	9.05	9.74
GO	M	7.45	8.45	9.70	12.56	11.00	9.83
	F	7.23	9.03	9.82	10.40	9.06	9.12
PO	M	9.83	10.00	11.96	11.86	15.46	11.73
	F	7.10	8.67	8.49	11.58	12.20	9.61

TABLE 5.67: HOMINOIDS: MEAN VALUES OF PERCENTAGE SEXUAL DIMORPHISM

Sp	Mandible	Palate	Base	Vault	Face	Total Mean
HS	88.7	91.0	92.1	95.1	90.9	91.6
PA	94.5	97.1	94.2	95.2	94.0	95.0
GO	84.8	87.7	83.0	79.9	79.9	83.1
PO	86.4	84.1	88.0	89.7	81.8	86.0

values range from 84.8 % (GO) to 94.5 % (PA).

Figure 5.01 shows percentage sexual dimorphism for each species in the mandible where one hundred per cent represents the mean male value for any particular character. The divergent lines represent the mean female value in relative to the mean male value so when the two lines meet, the variable is not dimorphic for the species in question. Values are calculated using the formula: female mean/ male mean x 100 so that when the lines diverge below the 100 per cent line females are smaller than males for that character; when the opposite occurs, females are larger than males for that character.

Figure 5.1 demonstrates between species variability in sexual dimorphism for each variable (see table 5.03 for values) since the values for each character of each species are plotted. Overall, *Pan* seems to be the least dimorphic species in mandibular characters and *Gorilla* the most dimorphic although *H. sapiens* is the most dimorphic for M8 (internal breadth) and M10 (depth at M1). In variables M8 and M9 (external alveolar breadth) the four species are closest in their level of dimorphism but are within 10 units of each other in M1 (bigonal breadth) and M7 (corpus thickness). *H. sapiens*, *Gorilla*, and *Pongo* are closest in M11 (depth at M3) while *H. sapiens* and *Pan* are closest in M3 (length), M4 (minimum ramus breadth), and M12 (arcadal length). Thus *Pongo* and *Gorilla* are the most dimorphic species, *Pan* the least, and *H. sapiens* fluctuates between greater and lesser dimorphic characters.

5.16 Palate

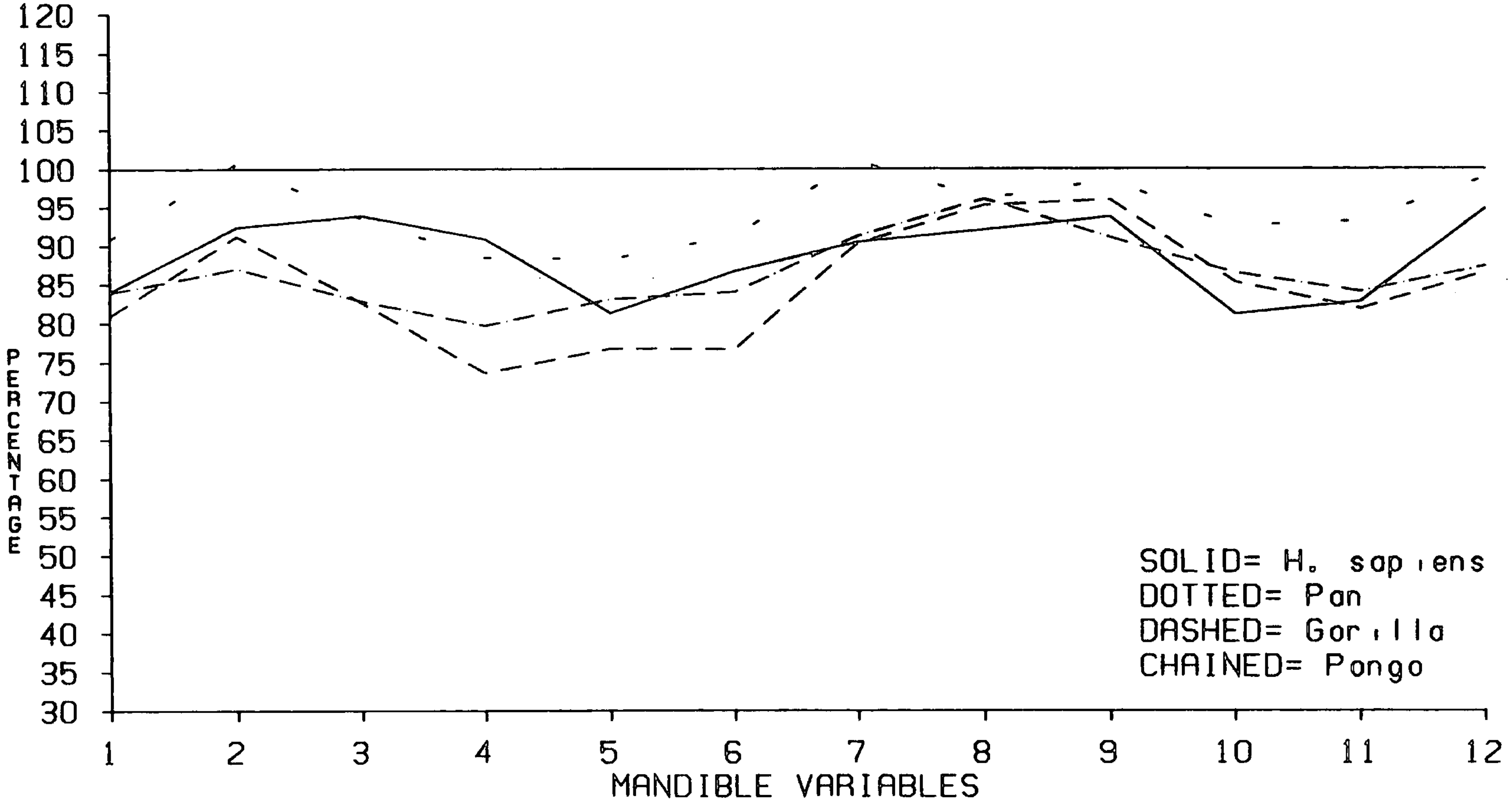
5.16.1 Variance

Pan and *Gorilla* have no significantly different variances but *H. sapiens* and *Pongo* both have one character which is significant but not the same one (see table 5.04, 5.17, 5.22, 5.27).

An examination of the values of CV for the palate shows that for P2 to P9 there is a considerable overlap of the ranges of the sexes (table 5.05). For P1 the species range is 8.33 (HS) to 13.55 (GO), the male range 7.05 (PO) to 9.42 (GO), and the female range 6.12 (PO) to 7.91 (PA). Thus there only is a partial overlap of the ranges with values for males ranging higher. For *Pongo* the values of males and females are the most similar whereas the *Gorilla* male value is 1.5 times greater than the female value, thus *Gorilla* contributes most to the difference in CV. The means for P1 are significantly different in all species except *Pan*.

A breakdown of the mean values of CV for the sexes for the palate (table 5.66)

FIGURE 5.01: PERCENTAGE SEXUAL DIMORPHISM: MANDIBLE



shows that the values for the sexes are similar within each species as well as between each species but for *H. sapiens* and *Pongo* the male values are greater than the female values.

5.16.2 Means

No means for *Pan* were significantly different but of those for the other species *H. sapiens*, *Gorilla*, and *Pongo* share 5 variables whose means are different (P1 - 4, P6) (table 5.04, 5.17, 5.22, 5.27).

Table 5.67 shows the mean values of percentage sexual dimorphism for the palate which range from 84.2 % (PO) to 97.1 % (PA).

Figure 5.02 represents percentage sexual dimorphism of the palate for the four modern species (see table 5.06 for values). *Pan* is the least dimorphic, *Pongo* then *Gorilla* the most dimorphic, with *H. sapiens* fluctuating in between. There are no characters where all four species have a similar level of dimorphism. *H. sapiens*, *Gorilla*, and *Pongo* have similar levels of dimorphism for three characters (P2, P4, P6). For P1 and P5 *Pan* and *H. sapiens* are at a similar level as are Pongo and Gorilla. For P3 each species is within 5 % of another species, for P7 and P9 *H. sapiens* and *Gorilla* are closest in value with *Pan* the least and *Pongo* the most dimorphic, and for P8 *Pan* and *Gorilla* are closest in value with *H. sapiens* slightly more dimorphic and *Pongo* greatly so; *Pongo* showing the greatest amount of dimorphism in characters P7 and P8.

5.17 Base

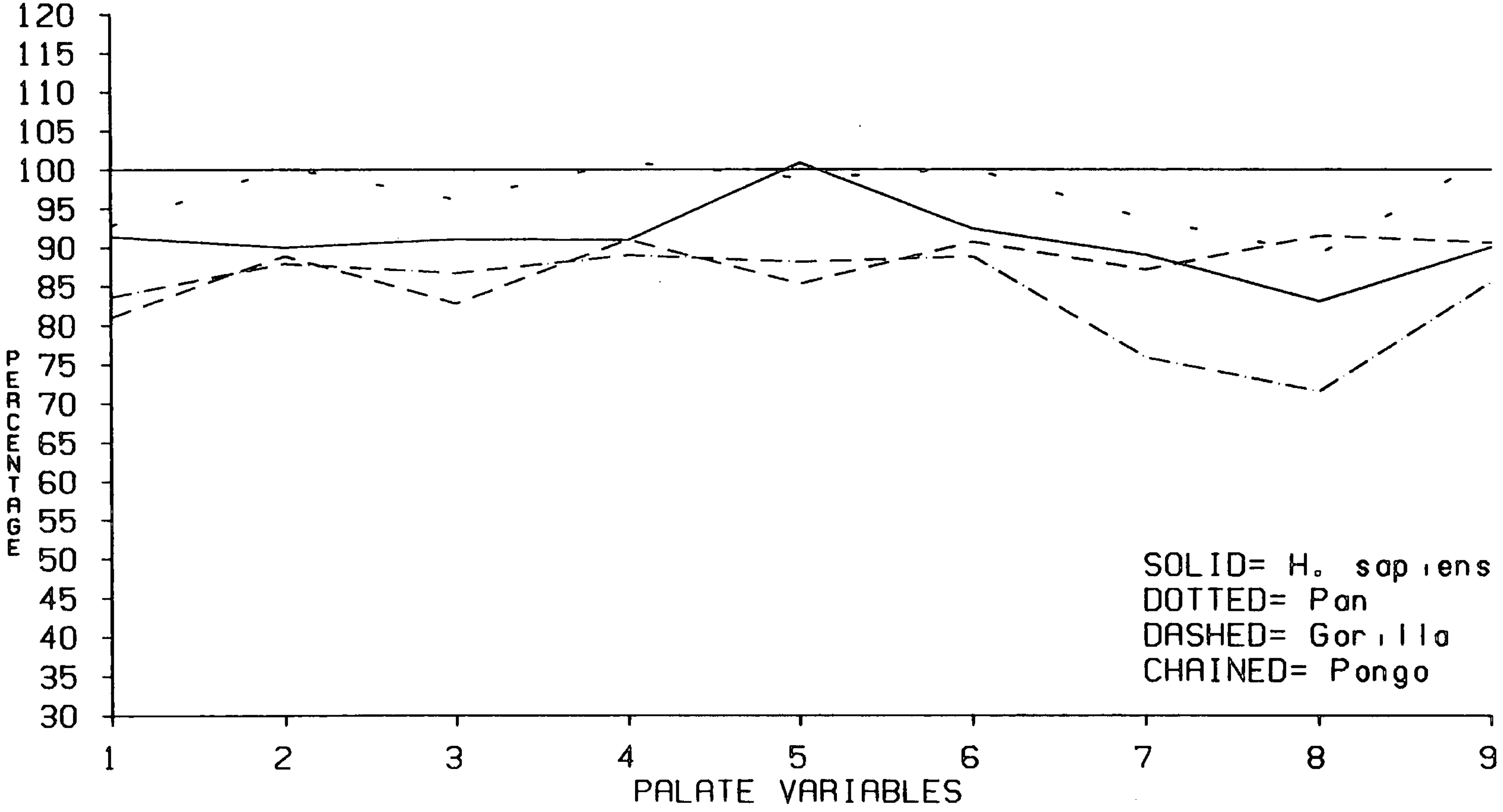
5.17.1 Variance

Pongo and *Pan* both have a significant difference in variance for the variables B21 - 23 (table 5.07, 5.18, 5.23, 5.28). Examining table 5.08 one can see that in all but two measurements the ranges of the values of CV for the sexes overlap considerably. For B2 the range of the species is 7.72 (HS) to 10.31 (GO), the male range 4.90 (GO) to 6.76 (PA), and the female range 9.02 (HS) to 11.74 (PO). Thus there is no overlap in the ranges of the sexes for this variable.

For B11 the species range is 7.93 (PA) to 13.51 (HS), the male range 8.28 (GO) to 16.39 (HS), and the female range 6.6 (PA) to 10.84 (GO) and so there is some overlap of ranges with male values ranging higher than female values.

The breakdown of mean values of CV for the Base (table 5.66) shows that the values are similar for the sexes within and between species but only for *Pongo* and

FIGURE 5.02: PERCENTAGE SEXUAL DIMORPHISM: PALATE



Pan does the male value exceed the female value.

5.17.2 Means

Characters that have a significant difference between the means are common in four cases to all four species (B3, B10, B15, B17). *H. sapiens*, *Gorilla*, and *Pongo* alone have six variables in common (B4, B5, B12, B14 B18 B22), and *Gorilla* and *Pongo* alone have eight variables in common (B6, B11, B13, B16, B19 - 21, B23). Thus *Gorilla* and *Pongo* show the most variability, followed by *H. sapiens* and then *Pan* (see table 5.07, 5.18, 5.23, 5.28).

Table 5.67 shows that the mean values of percentage sexual dimorphism for the base range from 83.0 % (GO) to 94.2 % (PA). Figure 5.03 demonstrates percentage sexual dimorphism for the base (see table 5.09 for values). *Pan* and *H. sapiens* are the least dimorphic for the base and *Gorilla* the most variable followed by *Pongo*. The characters which are closest for the four species are B1, B4, B5, B9 with B3, B6, B8, B10, and B11 within 10 units of each other. For B2 three species (HS, PA, and PO) are slightly dimorphic and *Gorilla* more so and for P7 the values range from *Pan* being the least to *Gorilla* being the most dimorphic. For B12 and B13 there is a split with *Gorilla* and *Pongo* more dimorphic and *Pan* and *H. sapiens* less dimorphic. For B14 the values for *Pan* and *Gorilla* are separated by those for *H. sapiens* and *Pongo* which are close in value and B15 shows *Gorilla* the most dimorphic with the other species having similar levels of dimorphism. *H. sapiens* and *Pan* have similar values for B16, B17, and B18 with *Pongo* then *Gorilla* being more dimorphic; for B19 *H. sapiens*, *Pan*, and *Pongo* have similar values with *Gorilla* the most dimorphic; and for B20 *H. sapiens* and *Pan* are only slightly dimorphic with *Pongo* and *Gorilla* being moderately and greatly dimorphic respectively. *Pan* and *H. sapiens* are slightly dimorphic for B21 and 22 while *Gorilla* and *Pongo* are moderately dimorphic. B23 is highly dimorphic for all four species, with *H. sapiens* the least and *Gorilla* the most dimorphic for this character and B24 is highly dimorphic for *H. sapiens* but not the other three species.

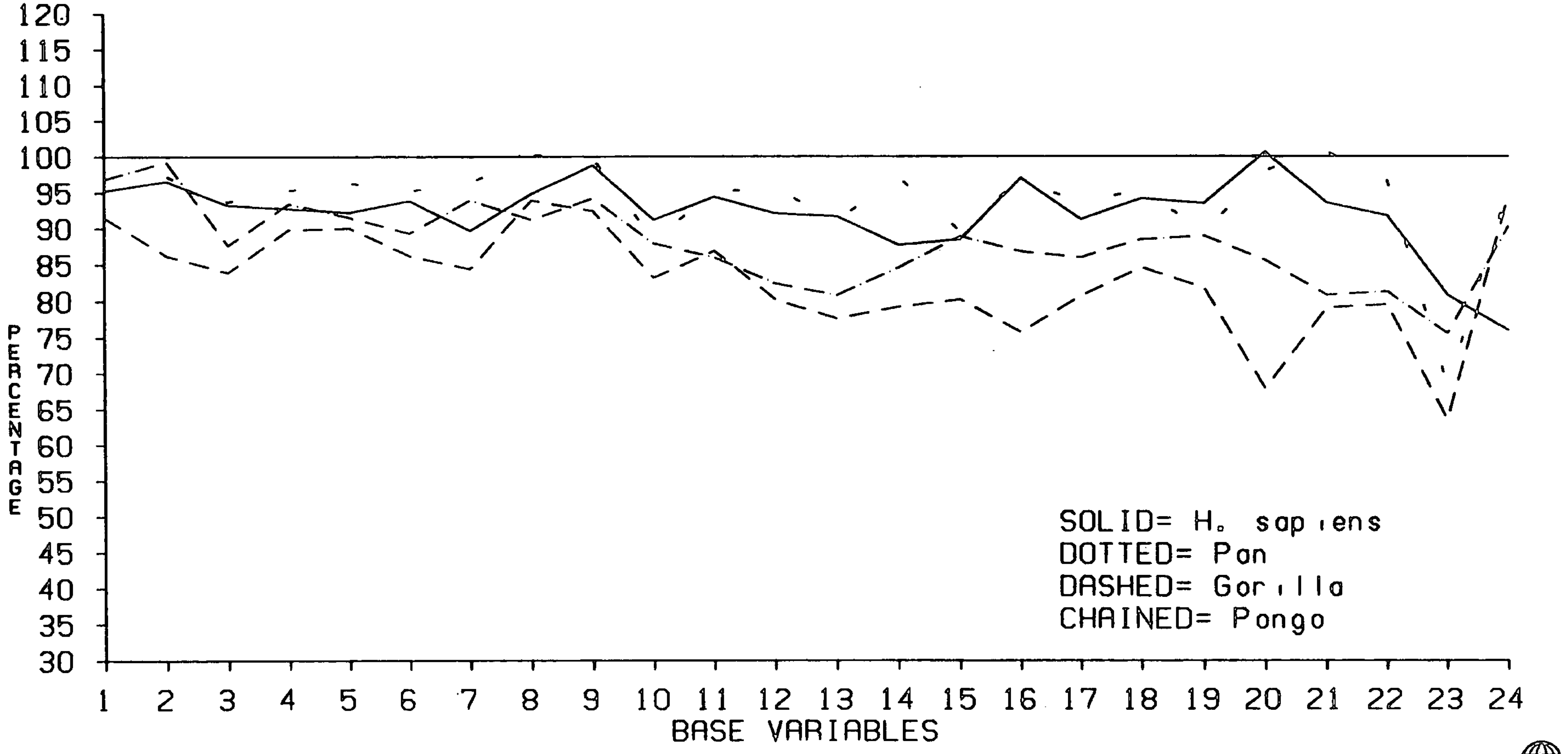
5.18 Vault

5.18.1 Variance

Gorilla and *Pongo* share three variables (V13, V15, V21) which have a significant difference in variance (see table 5.10, 5.19, 5.24, 5.29).

In all cases the ranges of CV of the sexes overlap (see table 5.11). For V2, V7,

FIGURE 5.03: PERCENTAGE SEXUAL DIMORPHISM: BASE



V9, V18, V19, V21, and V22 the male range overlaps the female range but the female range is smaller than that of the males. In the case of V7 the values for male Gorillas increase the male range due to the effect of the sagittal crest.

An examination of table 5.66 shows that the mean values of CV for the base are similar within and between species but male values exceed female values in *Gorilla* and *Pongo* samples.

5.18.2 Means

There are five variables with a significant difference between the means shared by all four species (V16, V17, V19, V20, V22) one by *Pan*, *Gorilla* and *Pongo* (V15), four by *H. sapiens*, *Gorilla*, and *Pongo* (V9, V18, V21, V24), one by *Gorilla* and *Pongo* (V14), one by *Pan* and *Gorilla* (V3), and one by *H. sapiens*, *Pan*, and *Gorilla* (V4) (see table 5.10, 5.19, 5.24, 5.29).

The mean values of percentage sexual dimorphism for the vault range from 79.9 (GO) to 95.2 % (PA) (see table 5.67). Figure 5.04 represents percentage sexual dimorphism for the vault (see table 5.12 for values). *Pan* is the least dimorphic species followed closely by *H. sapiens* and *Pongo* but *Gorilla* is highly dimorphic in the vault. The four species have similar levels of dimorphism for six variables (V1, V2, V5, V6, V9, V10) and V17 and V18 are just over ten units apart. For V3 and V4 all but *Gorilla* are only slightly dimorphic; for V11 - 13, *H. sapiens*, *Pan*, and *Pongo* have a similar level of dimorphism but *Gorilla* is highly dimorphic for these variables; V14 is not a dimorphic character for *H. sapiens* but is for *Pan* and *Pongo*, which have similar values, and *Gorilla*; V15 and V16 show *Pan* and *H. sapiens* at similar levels of dimorphism with *Pongo* and *Gorilla* more dimorphic for these characters; V19 - 22, and V24 show *H. sapiens* and *Pan* with similar levels of dimorphism; and for *Gorilla* and *Pongo* V19, V20, V22, and V23 levels of dimorphism are similar but for V21 and V24 the value for *Pongo* is closer to the other species and *Gorilla* is the most dimorphic.

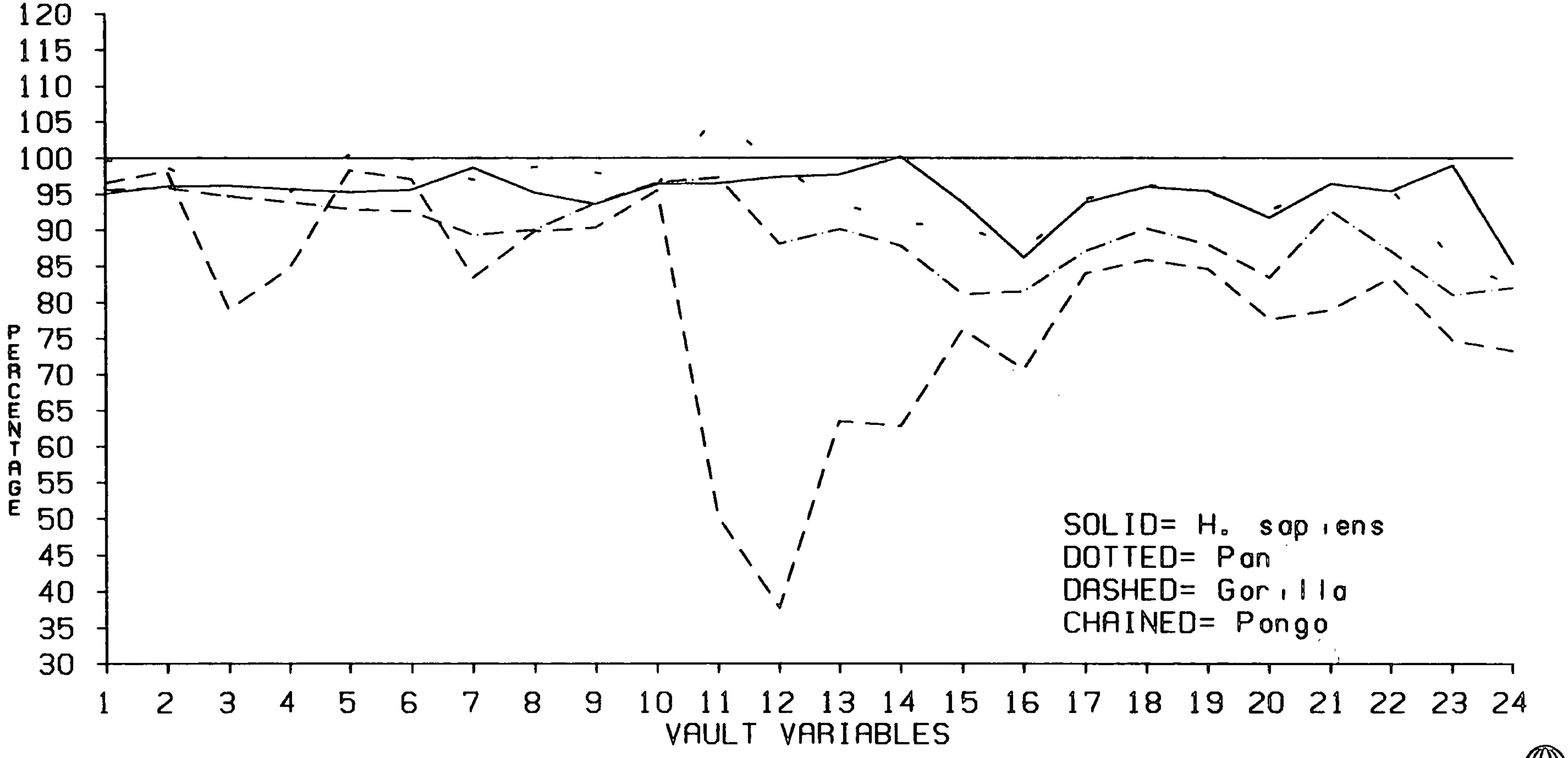
5.19 Face

5.19.1 Variance

There are three variables with a significant difference in variance shared by *Gorilla* and *Pongo* (F3, F22, F25), one character shared by *Pan* and *Pongo* (F9), and one by *Pan* and *Gorilla* (F12) (see table 5.13, 5.20, 5.25, 5.30).

Most of the ranges of CV for the sexes overlap for each variable. For F11, F17 and F20, females are less variable than males but male values range higher. For F23

FIGURE 5.04: PERCENTAGE SEXUAL DIMORPHISM: VAULT



the difference between the sexes is caused by *Gorilla* where the male value is 3.5 times greater than the female value but for the other species the values of the sexes are similar.

The breakdown of mean values of CV (see table 5.66) shows that within species there is not much difference between the sexes but between species the value for males is smallest in *H. sapiens* and largest in *Pongo* and for females is smallest for *Pan* and *Gorilla* and largest for *Pongo*. In *Pan*, *Pongo*, and *Gorilla* the male values exceed the female values.

5.19.2 Means

In five cases all the species have means that are significantly different (F1, F6 - 8, F23), *Pan*, *Gorilla*, and *Pongo* in five cases (F3, F9, F11, F26, F27), *H. sapiens*, *Gorilla*, and *Pongo* in ten cases (F12 - 14, F17 - 20, F22, F24, F25), *Gorilla* and *Pongo* in three cases (F2, F10, F21), *H. sapiens*, *Pan*, and *Gorilla* in one case (F5), and *H. sapiens* and *Gorilla* in one case (F16) (see table 5.13, 5.20, 5.25, 5.30).

Table 5.67 shows the mean values of sexual dimorphism for the four species which range from 79.9 % (GO) to 94.0 % (PA). Figure 5.05 represents percentage sexual dimorphism for the face (see table 5.15 for values). *Pan* is the least dimorphic species in the face followed by *H. sapiens*, then *Pongo*, and then *Gorilla* which is the most dimorphic in this region. The four species have similar levels of dimorphism in six variables (F1, F3, F4, F14, F17, F23). For F6 - 13, F18, F21, F22, and F25, *H. sapiens* and *Pan* have similar levels of difference between the sexes as do *Gorilla* and *Pongo*; for F15 *H. sapiens* and *Pan* still have similar values but *Pongo* is much more dimorphic than *Gorilla*; for F16 *Pan* and *Pongo* are not dimorphic but the other species are; for F19 and F20 *Pan* is not dimorphic, *Pongo* and *Gorilla* have similar values, and the values for *H. sapiens* approach those for the latter two species; for F24, *Pan* is the least dimorphic, *H. sapiens* and *Pongo* have similar values, and *Gorilla* is the most dimorphic; and for F26 *Pan* females are larger than males but the other species show similar values for this variable. As discussed in previous sections this latter character is very variable and also only reflects the size at the zygomatic suture which is not necessarily the maximum depth of the zygomatic arch. For F27 *Pan*, *Gorilla*, and *Pongo* are the most dimorphic and *H. sapiens* the least dimorphic.

5.20 Discussion

5.20.1 Sexual Dimorphism

In the majority of traits, males are larger than females but the degree of sexual

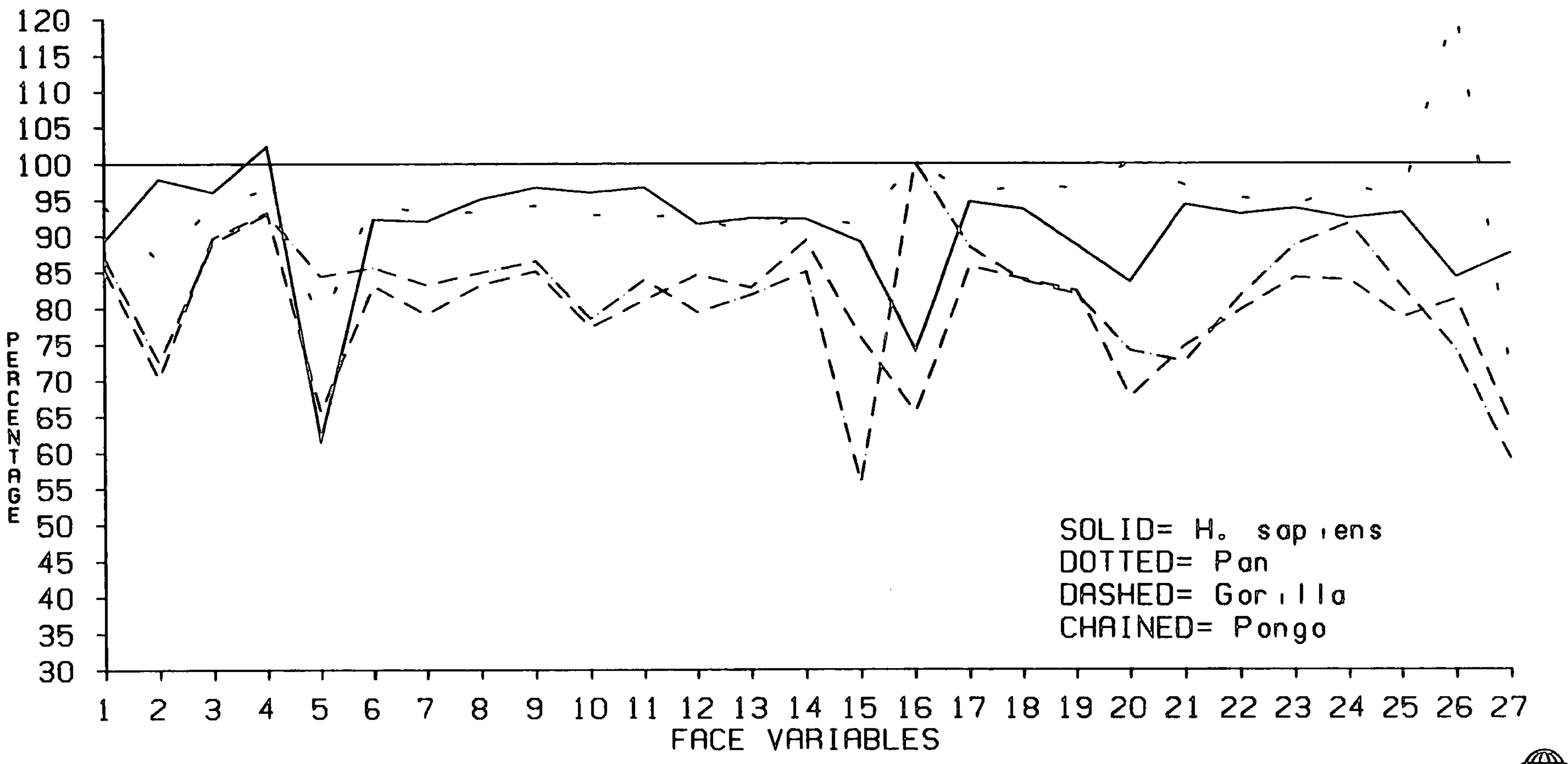


FIGURE 5.05: PERCENTAGE SEXUAL DIMORPHISM: FACE

dimorphism in each species varies. The degree of sexual difference for any one character is variable but, in general, more variables are dimorphic for *Gorilla* and *Pongo* than in *Pan* and *H. sapiens.* In the mandible, for example, the most dimorphic character is M5 (symphyseal height) for all four modern species with values of percentage sexual dimorphism ranging from 76.8 (GO) to 88.3 % (PA). *Pan*, suprisingly, is the least dimorphic species overall, followed by *H. sapiens*, with *Gorilla* and *Pongo* the most dimorphic, a situation reflected in the mean values of CV (see table 5.66), the mean values of percentage sexual dimorphism (see table 5.67), and the percentage of significant variances and means (see tables 5.68 and 5.69).

Where there is a significant difference in the variance between the sexes, males are generally more variable than females. The exceptions are V11 and V12 (inion chord and arc) for *Gorilla* where females are slightly more variable than males though both sexes have high values of CV; and in *Pan* M8, M9, B18, B21, B22, B23, and F12 are more variable for females than males. There are fewer significant sexual differences in variance than in means, and traits that show a difference in the former do not necessarily show a significant difference in the latter. *Gorilla* and *Pongo* show the most significant differences in the variance between the sexes while differences in the means are also most pronounced in *Gorilla* and *Pongo* and relate to absolute size difference between the skulls.

In the modern species, dimorphism is most pronounced in the areas of nuchal and temporal muscle attachment, the area of kyphosis of the base, the width of the palate, mandible, and base, and facial projection. This pattern of variation seems to be present in the hominid sample though a larger sample of complete cranial material would be needed to substantiate this apparent trend.

To devise a test of sexual differences in the early hominids is is a difficult proposition since the pattern within modern groups differs from species to species. For some variables there may be little or no difference in CV between males and females of one species, in another species the male value is considerably larger than the female value, and in a third species the female value for the same variable can exceed that for the male. For example, for F12 the values of CV for male and female *H. sapiens* are very similar, for *Pan* the female value exceeds the male by 2.4 times, and the male *Gorilla* value exceeds the female value 3.6 times. Also, if male and female values of CV for the four species are combined so that the lowest value of one sex of one species and the highest value of the same sex for another species provide the sex range for that variable, there is a tendency for the ranges of the two sexes to overlap. This means that the lowest female and lowest male values and highest male and female

TABLE 5.68: HOMINOIDS: BREAKDOWN OF PERCENTAGE SIGNIFICANT VARIANCE

	HS	PA	GO	PO
Measurements	1.0	9.4	21.9	25.0
N=96				

TABLE 5.69: HOMINOIDS: BREAKDOWN OF PERCENTAGE SIGNIFICANT MEANS

	HS	PA	GO	PO
Measurements	58.3	29.2	85.4	80.2
N=96				

values are very similar, and that there is no guarantee that high values of CV are more indicative of males rather than females. Thus there is no simple model of sexual dimorphism in variance for the higher primates with which to determine the sexes of fossil individuals and a more complicated assessment will not be undertaken in this thesis.

5.20.2 Homogeneity of Fossil Groups

A number of characters were considered to possess low percentage values of sexual dimorphism (percentage value of 85 % or greater) for the purposes of this study. The value of 85 % or greater was chosen arbitrarily as this value allowed approximately one third of the variables measured to be considered. In the mandible and palate these characters relate to the length and width of the dental arcade (maximum thickness of the mandibular corpus -M7, maximum internal breadth -M8, maximum external breadth -M9, arcadal length -M12, maximum lingual breadth -P2, maximum external breadth -P4, arcadal length -P5, maximum arcadal breadth -P6, and bicanine breadth -P9). In the base, characters of low dimorphism involve mainly the midline structures and include: foramen magnum length (B1), foramen magnum width (B2), bistylomastoid width (B4), bistyloid width (B5), bicarotid canal width (B6), biforamen ovale width (B8), biinfratemporal fossa width (B9), carotid canal to apex of the petrous temporal (B11), and bimastoid breadth (B18). Vault characters of low dimorphism (maximum frontal breadth -V1, maximum biparietal breadth -V2, frontal chord -V4, parietal arc -V5, parietal chord -V6, occipital chord -V8, basi-bregmatic height -V9, supraglabellare-bregmatic chord -V10, porion-dacryon chord -V18, and porion-zygoorbitale chord -V19) are ones which document the overall proportions of the skull but exclude characters from areas like the supraorbital region and nuchal areas which are variable for reasons given previously. Facial characters of low sexual dimorphism involve two areas: the orbits (biorbital breadth -F1, orbit breadth -F3, and maximum orbital height -F4); and the mid-face (bimaxillary chord -F9, nasal breadth -F14, and bizygomatic tubercle breadth -F17). The orbital characters presumably involve areas which are stable, ones on which stabilising selection is acting most strongly due to the functional requirements of these sense organs. The width of the mid-face is possibly correlated with basal characters and this may account for there being less difference between the sexes in this area.

A number of characters had low values of CV for both males and females including M3, M6, M9 - 11, P1 - 6, B1 - B9, B12, B17, B18, B22, V1, V2, V8, V9, V10, V17 - V22, F1, F3, F4, F6, F7, F8, F9, F11, F17, F18, F19, F22 - F25. Thus the characters which are the least dimorphic and with the lowest values of CV (within sexes and species) are M9, P2, P4, P5, P6, B1, B2, B4, B5, B6, B8, B9, B18, V1, V2, V8, V9, V10, V18, V19, F1, F3, F4, F9, and F17. For some of these characters there is a significant difference in the variance between the sexes of at least one species but they will still be included in the analysis since the value of CV for the species (sexes combined) is low. Characters for which there is a significant difference between the variances and the means of the sexes are excluded (V18, V19, F3, F9).

Characters are said to have high phyletic valence if they have low variability within groups but high variability between groups (Robinson 1960, 1965a; Tobias 1967). In order to test if the non-variable, non-dimorphic traits have phyletic valence the measurement values of these variables were pooled for *H. sapiens*, *Pan*, *Gorilla*, and *Pongo* to obtain values of CV for each variable (CV1), and then the measurement values of pongids alone were combined to obtain a second set of CVs (CV2) for each of these variables. Thus the combined measurement values of relatively invariant traits in relatively variable taxa provide values of CV known to represent two taxonomically diverse samples.

The values of CV1 and CV2 were then compared to those for modern and fossil groups (see table 5.70). In all but two cases the pooled values of CV are higher than those of the individual modern species CV values. For *Pongo* the value of CV for P2 is higher than both the combined values (CV1 and CV2) and the value of CV for V2 is slightly higher than the value of CV for the pooled pongid value (CV2).

The information in table 5.70 can be used to assess the homogeneity of the fossil samples: If the values of CV for a fossil sample are similar to those for the modern species for a particular character then there is no reason to conclude that more than one species is being sampled. However, if the value of CV is considerably greater than for the modern species, closer to the values of CV1 and CV2 (known to be specifically heterogeneous), then it is likely that something other than sexual difference is contributing to the variability since the variables used are ones known to be non-variable and non-dimorphic within modern hominoids. This is investigated below in sections 5.21-5.26 to test the homogeneity of the fossil samples.

5.21 Homo erectus

The *H. erectus* values of CV were compared to those of the modern species and to those of CV1 and CV2 for those variables found to be the least dimorphic and least variable in the previous section (see table 5.70). The value of CV for M9 (external breadth) is slightly higher than that for the modern groups, the raw measurement values ranging from 6.33cm (BK 67) to 7.6cm (OH 22) but the largest of these was

TABLE 5.70: HOMINOID, FOSSIL, AND COMBINED SAMPLE VALUES OF CV

VAR	CV1	CV2	HS	PA	GO	PO	HE	HH	AFAR	A.AFR	AR	AB
M9	10.23	9.39	6.09	5.37	4.18	6.45	6.86	6.29	13.02	9.24		9.84
P2	10.08	10.05	9.54	6.93	9.08	10.92		6.49	10.88	17.89	9.20	6.00
P4	10.01	10.17	6.71	5.68	6.75	8.27		13.06	5.69	10.07	6.65	1.88
P5	23.21	15.34	6.48	6.22	9.76	7.55		9.27	20.51	6.42	3.60	10.79
P6	9.46	10.03	5.67	5.31	6.70	7.88		9.79	6.18	12.63	7.35	5.92
B1	12.99	12.05	10.52	11.02	7.44	11.76	12.72	4.26		4.88		2.24
B2	12.44	12.20	7.72	9.31	10.31	9.16	11.16	4.20		11.64		10.71
B4	13.50	12.61	7.12	5.68	7.85	7.16	6.21	7.06		1.53		7.67
B5	14.68	10.12	7.85	6.06	8.16	8.81	7.83	7.57		3.36		9.94
B6	15.90	11.99	8.97	6.47	10.87	9.48	7.77	13.00		7.73		24.34
B8	11.59	12.04	7.30	6.47	7.64	8.10	5.34	20.15		7.27		16.84
B9	14.14	10.25	7.19	5.38	7.02	9.60	16.72	12.18		4.55		3.35
B18	14.53	16.37	6.57	8.82	10.31	9.88	7.05	7.45		5.07		21.79
V1	20.94	6.84	4.91	4.25	5.95	6.87	5.74	8.61		17.79		3.19
V2	17.84	6.35	4.69	4.22	6.19	6.01	3.44	7.69	8.50	8.73		7.44
V8	25.95	14.35	5.98	7.95	9.55	11.62	10.10	21.15		7.13		3.69
V9	16.60	8.88	4.82	4.12	7.02	6.90	3.71	2.12		7.60		9.19
V10	28.23	10.33	6.13	7.99	8.63	6.74	12.66	5.81		21.21	35.00	30.43
F1	12.94	14.36	4.59	5.41	9.29	9.11	1.37	3.68		7.11		9.02
F4	11.25	11.45	4.09	7.10	8.28	6.59	1.66	5.59		2.83		9.41
F17	15.10	15.63	5.59	5.25	9.79	9.61	10.03	11.44		8.70	5.49	14.18

CV1 = CV FOR COMBINED SAMPLE OF HS, PA, GO, AND PO

CV2 = CV FOR COMBINED SAMPLE OF PA, GO, AND PO estimated. The B1 (foramen magnum length) value of CV is also slightly higher than that of CV2 (pongid values combined) with KNM-ER 3733 and 3883 having closer raw measurement values to one another than either does to SANGIRAN 17. *H. erectus* has a CV of 12.72 (n=3) for B1 which falls within the confidence intervals of *Pongo* (7.8-15.7), *Pan* (7.3-14.7), and *H. sapiens* (6.8-14.3), but also within those of CV1 (pongid and human values combined) (10.9-15.1) and CV2 (9.8-14.3). Thus these results are equivocal.

For B2 (foramen magnum width), KNM-ER 3733 and SANGIRAN 17 have similar raw measurement values with that of KNM-ER 3883 being smaller. *H. erectus* (n=3) has a CV of 11.16 for B2 which falls within the confidence intervals of *Gorilla* (8.6-12.0) and *Pan* (6.2-12.4) as well as those of CV1 (10.4-14.5) and CV2 (9.9-14.5). Thus the results for this variable are also equivocal.

The *H. erectus* value of CV for B9 (biinfratemporal fossa width) exceeds the modern values of CV but the highest raw measurement value in this sample was estimated. For this variable KNM-ER 3733 and 3883 have similar raw measurement values, as do OH 9 and SANGIRAN 17.

For V10 (supraglabellare-bregma) the skulls divide, on the basis of the raw measurement values, into two groups of African and Asian specimens. This causes a higher value of CV in *H. erectus* for this variable than found in the modern species. *H. erectus* (n=10) has a CV of 12.66 for V10 and this value falls outside the confidence intervals of *H. sapiens* (4.1-8.2), *Pan* (5.3-10.6), *Gorilla* (5.7-11.5), *Pongo* (4.5-9.0), and CV2 (8.4-12.2) although it falls below the interval for CV1 (23.5-33.0). The confidence interval for the *H. erectus* sample (6.1-19.2) overlaps with those of the modern samples but also with that of CV2 which is known to represent a taxonomically diverse sample. The fact that the sample size of *H. erectus* for this variable is only half that for the modern species but has a high value of CV indicates that the sample might well be heterogeneous. Similarly, the fact that the sample can be divided into two groups of African and Asian specimens on the basis of the raw measurements reinforces this hypothesis.

For F17 (bizygomatic tubercle breadth) only two specimens were measured. *H. erectus* has a CV of 10.03 for this variable which falls within the confidence intervals of *Pongo* (6.4-12.8) and *Gorilla* (6.5-13.1) but not within the intervals of CV1 (12.6-17.6) or CV2 (12.7-13.1). Thus this variable cannot be used to challenge the homogeneity of the *H. erectus* sample, the limited sample size reducing its utility.

An examination of the characters which were the least variable showed no great discrepancies between the values of CV for *H. erectus* and those of the modern species. Some of the differences may be due to error in measurement as some values were estimated but the CV for V10 may be indicative of regional differences between African and Asian *H. erectus*.

5.22 Homo habilis

H. habilis showed some discrepancy between its values of CV and those of the modern species in nine cases (see table 5.70). Of the nine cases where CV exceeds the modern range two can be discounted (P4, P6). For P4 and P6 KNM-ER 1813 has the largest raw measurement value but the palate of this specimen is damaged and these values were estimated.

For B6 (bicarotid canal width), *H. erectus* has a CV of 13.0 which falls within the confidence intervals of *Gorilla* (7.2-14.5) but also within that of CV2 (9.8-14.2). While these results are inconclusive, it should be noted that the CV for *H. habilis* is almost twice that for *H. erectus* (CV=7.77) for this variable and that the B6 measurement is estimated on KNM-ER 1470.

For B8 (biforamen ovale width), the lowest and highest raw measurements were estimated and this may have caused the high value of CV (20.15) for *H. habilis*. This value of CV lies well outside the confidence intervals of all the comparative samples and is almost four times the value of CV of *H. erectus*. Thus this variable's CV may be an indication of heterogeneity of the *H. habilis* sample, however the possibility of over or underestimated measurement values must be acknowledged.

The lowest raw measurement for B9 (biinfratemporal fossa width) was estimated and this may have contributed to the high value of CV for *H. habilis* (n=5). This value of CV (12.18) lies within the confidence limits of *Pongo* (6.4-12.8) but also within that of CV1 (11.9-16.4) thus the result is equivocal.

The lowest raw measurement for V1 (frontal breadth) was also estimated and this may be the reason for the high CV of *H. habilis* compared to those of the modern comparators. For V1, *H. habilis* (n=6) has a CV of 8.61 which falls within the confidence interval of *Pongo* (4.6-9.2) but outside that for CV2 (5.6-8.1) which is interesting since CV2 represents the diverse sample of *Pongo*, *Gorilla*, and *Pan*. Also, it should be noted that the CV for *H. erectus* (n=10) is 5.74. This either indicates that the sample of *H. habilis* is heterogeneous or, perhaps, that it is a highly dimorphic species like *Pongo*.

The raw measurements of V2 (biparietal breadth) have a range of 9.7cm (KNM-

ER 1813) to 12.05cm (KNM-ER 1470). The CV of *H. habilis* for V2 is 7.69 (n=6) which falls within the confidence intervals of *Pongo* (4.0-8.0), *Gorilla* (4.1-8.2), but outside that of CV2 (5.2-7.5). *H. erectus* (n=10) has a CV of 3.44 for V2, therefore *H. habilis* is more than twice as variable in this character as *H. erectus.* This may indicate that the *H. habilis* sample is either dimorphic, like *Gorilla* and *Pongo*, or heterogeneous.

For V8 (occipital chord), *H. habilis* (n=2) has a CV of 21.15 which is quite high, almost falling within the confidence interval of CV1 (21.6-30.3). Out of interest, I calculated the CV for the largest male and smallest female *Gorilla* for this variable, with a result of 17.02. Thus the two *H. habilis* specimens are more dispersed than *Gorilla* for this character. The two *H. habilis* specimens in question are KNM-ER 1813 and OH 24. This result supports Stringer (1987), Chamberlain (1987) and Chamberlain and Wood (1987) who would place these two specimens in different species of 'early *Homo*'.

For F17 (bizygomatic tubercle breadth), *H. habilis* (n=4) has a CV of 11.44 which falls within the confidence intervals of *Pongo* (6.4-12.8) and *Gorilla* (6.5-13.1) and not within those of CV1 (12.6-17.6) or CV2 (12.7-18.6). Therefore this variable cannot be used to challenge the homogeneity of the *H. habilis* sample.

The other variables examined fell within or below the modern range but the values of CV were not consistently close to any one species.

Since there is some indication that this sample is too variable to encompass one species it is worthwhile determining whether there are any consistent groupings of individual specimens (as for *H. erectus* and V10). KNM-ER 1805, OH 24, and SK 847 group together for B8, B6, and B9 and KNM-ER 1813 and 1470 for B6 and B9. For V1, OH 24, OH 16, and KNM-ER 1813 group together as do KNM-ER 3732, 1805, and 1470 whereas for V2, KNM-ER 1805 and 1813 have low values, KNM-ER 3732 and OH 16 have intermediate values, and those of KNM-ER 1470 and OH 24 are large. For F17 (bizygomatic tubercle breadth) KNM-ER 1813 is the smallest with KNM-ER 1470, OH 24, and SK 847 having similar values.

Unfortunately, there is no consistent grouping of individuals for these characters, so no attempt can be made here to subdivide *H. habilis.* However, these data provide some support for the suggestion made by other workers that *H. habilis* should be subdivided into different species (eg. Stringer 1986; Chamberlain 1987, 1989; Chamberlain and Wood 1987).

5.23 A. afarensis

Of the measurements listed in table 5.70, only six could be measured on any *A. afarensis* specimens. One of these six characters, M9 (external breadth), has a high value of CV but 6 out the 8 individuals measured for this character have estimated raw measurement values. Of the remaining five characters, only two, P5 and V2, have larger values of CV than those of the modern comparators. For P5 and V2, only three specimens could be measured, one of which was the reconstructed cranium.

A. afarensis (n=3) has a CV of 20.51 for P5 (arcadal length) which falls within the confidence interval of CV1 only (19.0-27.4). This value of CV is more than twice than that of *H. habilis* for the same character (9.27, n=4), a sample which may contain specimens of different species (KNM-ER 1805, 1813, OH 24, SK 847). Also, when a CV is calculated for the two largest *Gorilla* males and the smallest *Gorilla* female, the result is 17.7. Therefore the CV of *A. afarensis*, consisting of A. L. 199.1, 200.1, and the reconstructed cranium is not just the result of differences between males and a female of the same species, unless of course *A. afarensis* is more sexually dimorphic than *Gorilla*, a species shown above to be the most dimorphic of the modern comparators (percentage sexual dimorphism of *Gorilla* for P5 is 85.3 per cent). If these specimens all belong to the same species then the level of sexual dimorphism in *A. afarensis* must be greater than that found in the sample of *Gorilla* used in this study.

For V2 (biparietal breadth), the value of CV is 8.5 (n=3) which lies outside the confidence intervals of the modern species and that of CV2 (5.2-7.5) but is less than that of CV1 (14.9-20.8). *Gorilla* is not dimorphic for this variable (percentage sexual dimorphism = 98.2) and the largest and smallest raw measurements of this species are both those of males. A CV calculated from these measurements is 13.7, therefore it is possible that A. L. 162.28 and 333.45 are males of the same species since A. L. 333.45 and the reconstructed cranium are presumed males.

There is little evidence for heterogeneity of the *A. afarensis* sample since the only specimens which may not belong together in the same species are A. L. 199.1 and 200.1. However, claims of high levels of sexual dimorphism within *A. afarensis* as an explanation for the range of variation within the sample may only be valid if one allows for a greater level of sexual dimorphism than found in modern *Gorilla*.

5.24 A. africanus

M9 (external alveolar breadth) is a character of low variance and dimorphism for the modern comparators which has a high value of CV in *A. africanus* (see table

5.70) but the smallest value was estimated. P2 (internal breadth) has a high value of CV where MLD 6 and STS 52 have low values and STS 53, STS 5, and MLD 9 have higher values while that of STW 73 is intermediate but the lowest and highest values were estimated. The value of CV for P4 (external alveolar breadth) is outside the modern range and is larger than CV1 but the lowest value was estimated. For P6 (arcadal breadth) the CV exceeds CV1 and CV2 where MLD 6 and STS 52 have low values and STS 53 and MLD 9 have higher values but the lowest and highest values were estimated. The value of CV for B2 (foramen magnum width) exceeds the modern range but the value of MLD 37/38, when remeasured, was found to have been overestimated and a smaller value for this individual brings the CV within the modern range of values. For V1 (frontal breadth) the smallest measurement was estimated.

For V10 (supraglabellare-bregma chord), *A. africanus* has a CV of 21.21 (n=2) which is closer to the confidence interval of CV1 (23.5-33.0) than to CV2 (8.4-12.2) or those of the modern comparators. The CV calculated from the largest male and smallest female *Gorilla* is 21.82 (percentage sexual dimorphism for *Gorilla*= 95.5). So this might explain the difference between the measurements of these specimens if they are male and female *A. africanus*. However, the two specimens are STS 5 and STS 71, supposed females (Broom 1950). The CV calculated for the raw measurements of the largest and smallest female *Gorilla* is 17.45, therefore either 1) *A. africanus* has more variation in this variable than *Gorilla*; 2) the specimens are females of different species; or 3) STS 5 is a male.

In the majority of cases where the value of CV for *A. africanus* lay outside the modern range some raw values of the measurements were estimated. Thus there is not sufficient evidence to question the homogeneity of this species.

5.25 A. robustus

Of the characters listed in table 5.70, *A. robustus* differed from the modern groups in its value of CV for only one character (V10) and for this measurement only two individuals were measured. For V10, *A. robustus* has a CV of 35.0 which lies outside the confidence interval of CV1 (23.5-33.0) and is larger than the CV computed for the largest male and smallest female *Gorilla* (21.9). Since SK 46 is a distorted cranium it is possible that the raw measurement of V10 was underestimated. Thus there is no basis for disputing the homogeneity of this sample on the present evidence.

5.26 A. boisei

An examination of the characters in table 5.70 shows 12 cases where *A. boisei* has larger values of CV than the modern groups (M9, P5, B2, B5, B6, B8, B18, V2, V9, V10, F4, F17). For M9 (external breadth) the raw measurement value of KNM-ER 3230 was estimated. For P5 (arcadal length) KNM-ER 3891 and 405 have similar raw measurement values and that of OH 5 is larger. The value of CV for P5 is 10.79 which falls within the confidence interval of *Gorilla* (6.3-13.2) but falls below those of CV1 (19.0-27.4) and CV2 (12.3-18.3).

For B2 (foramen magnum width), KNM-ER 406 has the largest raw measurement value, OH 5 the smallest, and KNM-ER 407 an intermediate value. The value of CV for B2 is 10.71 but this falls within the confidence intervals of *Pan* (6.2-12.4), *Gorilla* (8.6-12.0), and also those of CV1 (10.4-14.5) and CV2 (9.9-14.5), thus the results are equivocal.

For B5 (bistyloid width), KNM-ER 406 has the largest raw measuement value, KNM-ER 407 the smallest, and OH 5 an intermediate value. This variable has a CV of 9.94 which falls within the confidence intervals of *Gorilla*, *Pongo*, *H. sapiens*, and CV2, thus the results are equivocal.

A. boisei (n=4) has a CV of 24.34 for B6 (bicarotid canal width) which falls above the confidence intervals of CV1 (13.3-18.5) and CV2 (9.8-14.2) but KNM-ER 732 has a very low, estimated value for this variable. So either the measurement value of KNM-ER 732 has been underestimated or else this sample is heterogeneous.

For B8 (biforamen ovale width), *A. boisei* (n=4) has a CV of 16.84 which falls above the confidence intervals of CV1 (9.6-13.6) and CV2 (9.8-14.3). The CV calculated on the basis of the two largest and two smallest raw values of *Gorilla* is 10.6. KNM-ER 732 has an estimated value for this variable so either that value was underestimated or else the sample of *A. boisei* is heterogeneous.

B18 (bimastoid breadth) has a high CV (n=4) but both OH 5 and KNM-ER 732 measurement values are estimated ones.

For V2 (biparietal breadth) the results are equivocal since the CV of *A. boisei* (7.44) lies within the confidence intervals of *Gorilla* (4.1-8.2), *Pongo* (4.0-8.0), and CV2 (5.2-7.5). The same situation arises with V9 (basi-bregmatic height) where the *A. boisei* (n=2) CV (9.19) lies within the *Gorilla*, *Pongo*, and CV2 confidence intervals.

For V10 (supraglabellare-bregma chord), *A. boisei* (n=3) has a CV of 30.43 which lies within the confidence interval of CV1 (23.5-33.0). A CV calculated from the raw measurement values of the two largest *Gorilla* males and the smallest *Gorilla* female is 15.95 (percentage sexual dimorphism= 95.5). Thus either *A. boisei* is more sexually dimorphic for V10 than *Gorilla* or else the sample of *A. boisei* is heterogeneous.

The CV for F4 (maximum orbital height) (9.41) lies within the the confidence intervals of *Pan*, *Gorilla*, and CV2 therefore the result is equivocal.

A. boisei (n=3) has a CV of 14.18 for F17 (bizygomatic tubercle breadth) which lies within the confidence intervals of CV1 (12.6-17.6) and CV2 (12.7-18.6). A CV of 16.3 is obtained from the two largest males and smallest female *Gorilla* measurement values (percentage sexual dimorphism= 85.8). Thus *A. boisei* is less dimorphic for this variable than the sample of *Gorilla* used in this study.

In many cases it is KNM-ER 732 which differs most in its raw measurement values from the other specimens. When differences occur, the raw measurement values of KNM-ER 732 are lower than those of the other specimens. KNM-ER 732 is a partial cranium within only half the face present and many measurements taken on it were estimated. This weakens the evidence with which to challenge the homogeneity of this sample though there is some suggestion that either KNM-ER 732 is not a member of the species *A. boisei* or that *A. boisei* is more sexually dimorphic and/ or variable than is *Gorilla*.

5.27 Discussion

The homogeneity of these fossil species has been questioned by a number of workers. Depending on which characters are used in classification, *H. erectus* can either encompass both the early African forms and the later Asian specimens or be subdivided into two (or more) groups (Wood 1984; Andrews 1984; Stringer 1984; Bilsborough and Wood 1986). This study shows that there are some characters (M9, B1, B2, B9, F17) for which *H. erectus* (African and Asian combined) are too variable to be only one species, but for most of these characters the specimens do not divide by region. Only for one character (V10- supraglabellare-bregma chord) do the skulls divide by region. Thus there is some evidence to support a subdivision of African and Asian *H. erectus*.

The homogeneity of *H. habilis* has long been the subject of debate. Many workers maintain that these specimens should be subdivided into different species, but no consensus has been reached as to how this division should be made (eg. Groves and Mazak 1975; Wood 1978, 1990; Howell 1978a; Dean and Wood 1982b; Stringer 1986; Chamberlain 1987, 1989; Chamberlain and Wood 1987; Leakey *et al.* 1989). The results of this analysis do not help to resolve this problem. This collection of fossils is variable compared to modern species but this may indicate 1) either a species in transition (increased diversity prior to, or during, speciation); 2) mosaic evolution; or 3) more than one species. A multivariate analysis, examining a combination of characters, may help to resolve this situation and this is attempted in Chapter 6. However, there is evidence, based on the value of CV for V8 (occipital chord), that KNM-ER 1813 and OH 24 do not belong to the same species.

The homogeneity of *A. afarensis*, while supported by some workers (eg. Johanson and White 1979; White *et al.* 1981) has been challenged by a number or authors (Tobias 1980a; Olson 1981, 1985; Senut and Tardieu 1985). This study could not definitively resolve this issue due to the small number of specimens measured. However, the results do suggest that either A. L. 199.1 and 200.1 do not belong to the same species or else *A. afarensis* is more dimorphic than *Gorilla* in certain characters. A larger sample of *A. afarensis*, preferably using the original fossils, may provide more substantive proof of its heterogeneity (or homogeneity).

Recently, Kimbel and White (1988) suggested that the specimens of *A. africanus* may be heterogeneous and Clarke (1988) outlines evidence which seems to support this view. The present analysis, however, is not as conclusive as the above studies due to the large number of estimated measurements. If these measurements are and accurate representation of the variability of *A. africanus* then the suggestion of the above authors may be a valid one.

The results based on V10 suggest, however, that *A. africanus* is either more variable for this character than are modern species or else that STS 5 is a male. Kimbel and White (1988) maintain that STS 71 is a male based on facial robusticity and post-canine tooth size. They say that if STS 5 is a female, then the difference in facial prognathism between it and STS 71 is opposite to what is found in the great apes where females are less prognathic than males (cf. Wood 1976, Kimbel *et al.* 1984). Rak (1985) also suggests that STS 5 could be a male. Thus the results of this study provide additional evidence to question the sex allocation of STS 5.

The CV of *A. robustus* for the character V10 (supraglabellare-bregma chord) is large compared to the CV's of modern groups for the same character. The sample size for this measurement, composed of two individuals, is too small to support or refute the homogeneity of this species. It should be noted here, however, that dental evidence may support the division of the Swartkrans and Kromdraai hominids into *A. robustus* and *A. crassidens* (Grine 1981, 1988a; Jungers and Grine 1986).

The recently discovered fossil material (KNM-WT 17000, KNM-WT 16000) from West Turkana, Kenya, along with material from Omo (from below Member G of the

Shungura formation) has led some workers to support the hypothesis that *A. boisei* was polytypic in its early stages (eg. Suwa 1988; Dean 1988). Amongst the later specimens, *A. boisei* it sensu stricto, some of the smaller forms (eg. KNM-ER 732) have been designated as females (Howell 1978a; Walker and Leakey 1978). Studies of within-species variation in *A. boisei sensu stricto* suggest that despite some differences between specimens they can all be combined within a single, sexually dimorphic, species (Rak and Howell 1978; Rak 1983; Wood 1985). Chamberlain and Wood (1985), in their study of the hominid mandibular corpus, found a greater degree of sexual dimorphism in *A. boisei* than that found in modern gorillas, a result compatable with the present study. Either *A. boisei* possesses a degree of sexual dimorphism equal to or greater than that in *Gorilla*, or else, as suggested by the earlier material from East Africa, more than one species of *A. boisei* existed during the Plio-Pleistocene.

5.28 Conclusions

The pattern of the values of CV in the modern species has been used as a model to test the homogeneity of the fossil samples. Characters which were the least dimorphic and least variable for males and females within the modern groups were chosen, their phyletic valence assessed by combining the values of modern humans and pongids and pongids alone to obtain 'between species values' of CV. Thus the values of CV1 and CV2 represent samples known to be taxonomically diverse. When values of CV for these characters within the fossil samples fell within the range of those for the modern species or close to it then it was assumed that the sample was homogeneous. However, if the values of CV exceeded those for the modern species and fell within or above the ranges of CV1 and/ or CV2, then it was inferred that the differences within the fossil group were not sexual ones and that the group must be heterogeneous, especially if the CV's for an equal number of, and sex ratio of, *Gorilla* specimens were smaller than the values of CV for the fossil sample.

An examination of the fossil groups found some evidence to support the hypothesis that *H. erectus* was heterogeneous but the evidence was not strong enough for the other hominid groups to doubt their cohesiveness. For example, even if A. L. 199.1 and 200.1 do not belong to the same species, this does not prove that the remaining sample of *A. afarensis* is heterogeneous though it does show that *A. afarensis* as defined is heterogeneous.

The use of computed values of CV, known to represent taxonomically diverse samples of specimens, so far as I am aware, is a method not previously used in the study of fossil hominids. The values of CV1 and CV2 demonstrate clearly that even when taxonomic diversity is known to exist within samples, this is not necessarily revealed by values of CV. Miller (1991) claims that a CV of greater than 10 in a fossil hominid sample is not necessarily indicative of heterogeneity. I would now claim also, that values of CV less than 10 are not always evidence of homogeneity (see CV1 value for P6 and CV2 values for M9, V1, V2, and V9 in table 5.7).

In the next chapter, multivariate statistical techniques will be used to determine if characters used in combination can illuminate more clearly patterns of within- and between species variability in the early hominids.

Addendum to Chapter 5

It was not until after the submission of this thesis that I became aware of Miller's (1991) work. He maintains that values of CV and their confidence limits should be calculated using formulas which correct for small sample bias. The interpretation of the results of the present study will doubtless be enhanced by the use of such formulae, but their utilisation has not been common in palaeoanthropological analysis (see, for example, Stringer 1986, Lieberman *et al.* 1988, Wood 1985, Tobias 1987). Similarily, the present results may be modified by the use of statistics which test for the significance of differences between the values of CV. The use of such statistics will be utilised in future analyses of the above data.

CHAPTER 6: MULTIVARIATE ANALYSIS 1: PRINCIPAL COMPONENTS

6.1 Introduction

Multivariate techniques can be used to compare the range of variability of two or more species and their separation, and also provide useful graphical representations of their relationships and are valuable when comparing the relationships within and between groups. The advantage of using multivariate over univariate techniques is that they allow an assessment of a combination of variables and thus simplify the description and understanding of complex phenomena (Reyment *et al.* 1984).

Principal Components Analysis (PCA) is used to discriminate between individuals. It is used in this study to examine the fossil hominids using a combination of variables (see Chapter 4 for a detailed description of the technique). The modern comparator used in this analysis is *Gorilla* since this species is, according to the univariate analysis (Chapter 5), the most dimorphic of all the modern groups, and by using it as a comparator the sex and homogeneity of fossil groups can be assessed. That is, if *Gorilla* separates on an axis by sex, then so may some groups of fossils. If the dispersion within a fossil species is greater than that for *Gorilla* males and females then either the fossil sexual dimorphism is greater than that found in modern *Gorilla* or else the fossil group is heterogeneous. On some axes male and female *Gorilla* may not separate by sex but their pattern of variation may be used as a measure of homogeneity of the fossil groups. If fossils are more widely separated than male and female *Gorilla* in this instance, then either the fossils are more variable for these characters in combination, or else the sample is heterogeneous. This does **not** mean that fossil hominids are morphologically similar to *Gorilla*: there are obvious contrasts of neurocranial and facial proportions, with the lower face and jaws of the pongid dominated by large canines, whereas hominids have relatively small canines. Thus the *Gorilla* is used as a model for the **degree** of dimorphic variation expected within the samples of fossil hominids rather than as a means for necessarily establishing the **pattern** of fossil hominid sexual dimorphism.

The multivariate pattern of variation within *Gorilla* and the fossil hominids is examined by PCA using the correlation matrix of a number of the raw linear dimensions from each skull region. Since the SPSSX PCA program rejects individuals with missing values, the skull is examined in 6 analyses: Mandible, Palate, Base, Vault, Face, and a Regional Combination. From each set of analyses, plots of PCII with PCI and PCIII with PCI are prepared in all regions except the Mandible and

Regional Combination analyses where a plot of PCIV with PCI is prepared. In these latter regions four PC's are required to account for approximately 90 per cent of the total sample variance (as explained in Chapter 4). The proportion of total variance expressed by the first three (or four) Principal Components (PC's) is noted and an attempt made to identify characters contributing to each PC.

Due to the fragmentary nature of the fossils, the inclusion of all variables from each region would result in most fossils being rejected. Thus only a selection of variables are used in each section where characters are chosen in such a way as to maximise the number of fossil specimens with the minimum loss of information. In the regional combination analysis variables are chosen on the basis of the results of the univariate analysis of the previous chapter. Thus a number of characters are used which have demonstrated low values of CV and low sexual dimorphism within the sexual morphs of *H. sapiens* and the pongids. Again characters are excluded to maximise the number of fossil hominids which can be included in the analysis.

Each group is assessed on its separation on each axis, then by region. Finally, in the concluding section, comments are made on which hominids can be grouped together for the purpose of the Discriminant Function or Canonical Variate Analysis (CVA).

CVA of the raw (untransformed) data is used to examine the interrelationships between a number of groups and to represent these interrelationships graphically in the fewest possible dimensions (see Chapter 4 for a more detailed description of the technique). The axes of variation are chosen to maximise the separation between the groups, relative to the variation within each of the groups. CVA examines the degree of separation between groups identified at the outset of the analysis, and can then be used to allocate new individuals to one of the initial groups and to calculate probabilities of misclassification.

Fossil groups to be entered into the CVA are determined from the PCA analysis. Specimens not allocated to a fossil group initially are entered as individuals to determine which group they most closely resemble. Again, in this analysis individuals with missing values are rejected so the skull is examined in six analyses as above and the number of fossil specimens will be maximised as above.

Tables of the correlation matrices and the rotated Principal Component matrices used in the Principal Component Analysis can be found in Appendix 4A. Matrices of the correlation of each character with each Canonical Variate for each region can be found in Appendix 4B. Appendix 4C contains within-species correlation matrices for the modern comparators only.

The correlation matrix indicates the extent to which the original variables are correlated with one another. The PCA and CVA both collapse multiple correlated variables into an equal number of uncorrelated variables but with the variance redistributed, so that the first few variables account for the great majority of the original variation. According to Reyment *et al.* (1984:22) the PCA technique "is sensitive to differences in the scales of characters, which can then dominate the calculations, [so] it is often preferable to employ the correlation matrix" rather than the dispersion (or variance-covariance) matrix. The correlation matrix can also be used in CVA if, in the first stage of the analysis, involving the rotation of the original characters (with the latent vectors being those of the correlation matrix), the population means are standardised by the corresponding within-populations standard deviations (Reyment *et al.* 1984:54). Thus correlation matrices are provided in Appendix 4C to demonstrate the degree of correlation between characters within each of the modern species.

6.2 Results

6.2.1 Mandible

The first PCA is performed using eight mandibular characters chosen in order to maximise the number of fossils which can then be included in the analysis (M2- foramen mentalia breadth; M5- symphyseal height; M7- maximum corpus thickness; M8- internal alveolar breadth; M9- external alveolar breadth; M10- depth at M1; M11- depth at M3; M12- arcade length). The exclusion of four variables (M1, M3, M4, M6) increases the number of fossil hominids from 8 to 20 individuals. Tables containing the correlation matrix and the rotated PC matrix can be found in Appendix 4A.

The first four PC's account for 91.5 % of the total sample variance. PCI accounts for 49.5 %, PCII 26.3 %, PCIII 8.3 %, and PCIV 7.4 % of the total sample variance. The variables with the highest loadings on PCI are M5 (symphyseal height), M10 (depth at M1), M11 (depth at M3) and M12 (arcade length) and all the loadings on all the variables are positive. This PC probably describes size variation within the sample since the measurements are ones of depth along the corpus and the length of the tooth row. On PCII, variables with the highest loadings are M7 (corpus thickness) and M9 (maximum external alveolar breadth) and probably represent robusticity of the mandibular corpus. On PCIII the variable with the highest loading is M8 (maximum internal alveolar breadth) and may separate individuals on the basis of wider versus narrower mandibular angles. M2 (foramen mentalia breadth) has the highest loading on PCIV and may distinguish between larger, more robust mandibles and smaller ones; the symphyseal region being a butress to withstand stress during mastication where a larger mandible would require stronger butressing.

On axis I most *Gorilla* specimens lie in the lower right quadrant (see figure 6.01A). *Gorilla* females have a slightly wider range of scores than *Gorilla* males and the sexes are separated on this axis.

The six *H. erectus* specimens are located in the lower left quadrant. The range of PC scores for these specimens is less than for either sex of *Gorilla*. On the basis of size OH22 and HI are probably female and Mauer a male but the remaining specimens could be of either sex.

The two *H. habilis* specimens are separated by a greater distance than the two male *Gorilla* extremes but less than the two female *Gorilla* extremes. Thus they are either both females or else, as the size difference indicates, male (KNM-ER 1802) and female (KNM-ER 1805). However, on the basis of the braincase and palate it is unlikely that KNM-ER 1805 is a female and it has been suggested that this specimen has been affected by pathology (White, Johanson, and Kimbel 1981) (see also section 6.2.3).

For *A. boisei* there are three specimens located in the upper right quadrant. Their range of scores is less than that of *Gorilla* females and approximately the same as that of *Gorilla* males. All three mandibles are extremely large and none would articulate with KNM-ER 732, a presumed female *A. boisei*.

Seven *A. afarensis* specimens are included in this analysis, one being the reconstructed mandible. The range of scores, including this latter specimen, is greater than that for either *Gorilla* males or females but is less than that for the two sexes combined. A. L. 333w.60 has a smaller score on this axis than the reconstructed mandible (incorporating the former specimen). Any differences between the two are likely due to the fact that both are casts, more measurements were estimated on A. L. 333w.60, and the reconstruction may not be totally accurate. Excluding the reconstructed mandible, the range of PC scores for the *A. afarensis* specimens is about the same as that for *Gorilla* males. A. L. 288.1, 198.1, and 266.1 are possibly females and A. L. 333w.60, 207.13, and possibly LH 4 males due to their positions on axis I. If A. L. 333w.60 and LH 4 are both the same sex then the size dimorphism in the teeth of *A. afarensis* males is considerable.

STS 36 is the only *A. africanus* specimen that can be included in this analysis. On axis I it has a PC score similar to those of A. L. 333w.60, BK 67, and LH 4 and is possibly a male *A. africanus*. SK 12, the *A. robustus* specimen, has a PC score close

FIGURE 6.01A: MANDIBLE: PLOT OF PCII WITH PCI

```
    ++----+----+----+----+----+----+----+----+----+----+----+----++
   3+                                                             +
    |                                                             |
    |                                                             |
    |                                                             |
    |                                 N-[ER3230]                  |
   2+              [AL333W60]-K                                   +
    |                                                             |
    |                             M-[SK12]                        |
    |                                       N-[ER729]             |
    |                             N-[PENINJ]                      |
   1+       [AL207.13]-K                                          +
    |                                                             |
    |          [AL288.1]    [STS36]                               |
P   |                                         E                   |
C   |                K      L       K-[Recon.]                    |
I  0+      [ER1805]-J K-[AL266.1] J      F                        +
I   |                  K-[AL198.1] [ER1802]   E       E           |
    |          [BL8518]-I I-[BK67]F                               |
    |       [OH22]-I    [LH4]-K     F  F          E               |
    |                     I  F      FF   F     E  E E             |
  -1+         [ER730]-I   [MAUER]    F            E               +
    |           [HI]-I                     E                      |
    |                                         E                   |
    |                                                             |
    |                               F                             |
  -2+                                                             +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
    -3        -2        -1         0         1         2         3
                                  PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

to that of Peninj on axis I and is probably a male *A. robustus*.

On axis II the PC scores of male and female *Gorilla* overlap and the range of scores of the sexes are about the same (see figure 6.01A). The *H. erectus* and *A. boisei* specimens both have a smaller range of scores than either sex of *Gorilla*.

For *A. afarensis* the range of scores exceeds that for *Gorilla*. All of the measurements for these variables are estimated except those taken on the reconstructed mandible. If they are accurate, however, *A. afarensis* is either more variable than *Gorilla* or all do not belong to the same species. If A. L. 288.1, 266.1, and 198.1 are from the same species then LH 4, but not A. L. 207.13 and 333w.60, could belong to it. If A. L. 207.13 also belongs to the above species, then neither LH 4 nor A. L. 333w.60 fall within that species range of variation (assuming that the *Gorilla* range provides the maximum limits of the *A. afarensis* range). It is likely that A. L. 288.1, 266.1, and 198.1 are females. A. L. 207.13 and 333w.60 have high values on this axis, as do *A. boisei* and *A. robustus*, and are probably males.

On axis II *H. erectus* have negative scores like *Gorilla*, but *A. boisei* and SK 12 have high positive scores reflecting the thicker and relatively wider mandibles of *A. boisei* and *A. robustus*. The *H. habilis* and *A. africanus* specimens have scores similar to some of the *A. afarensis* specimens.

On axis III the male *Gorilla* range totally overlaps that of the female range of PC scores (see figure 6.01B). *A. boisei* and *H. erectus* have a smaller range of scores than *Gorilla* males. The range of scores for *A. afarensis* exceeds that of *Gorilla* males but the value for A. L. 198.1 is estimated. This axis does not really discriminate between groups. Instead it shows a general trend from narrower (*A. afarensis*), to intermediate (*H. erectus*, *H. habilis*, *Gorilla*) to wide (*A. africanus*, *A. robustus*, *A. boisei*) mandibles, although the scores of each of these species overlap.

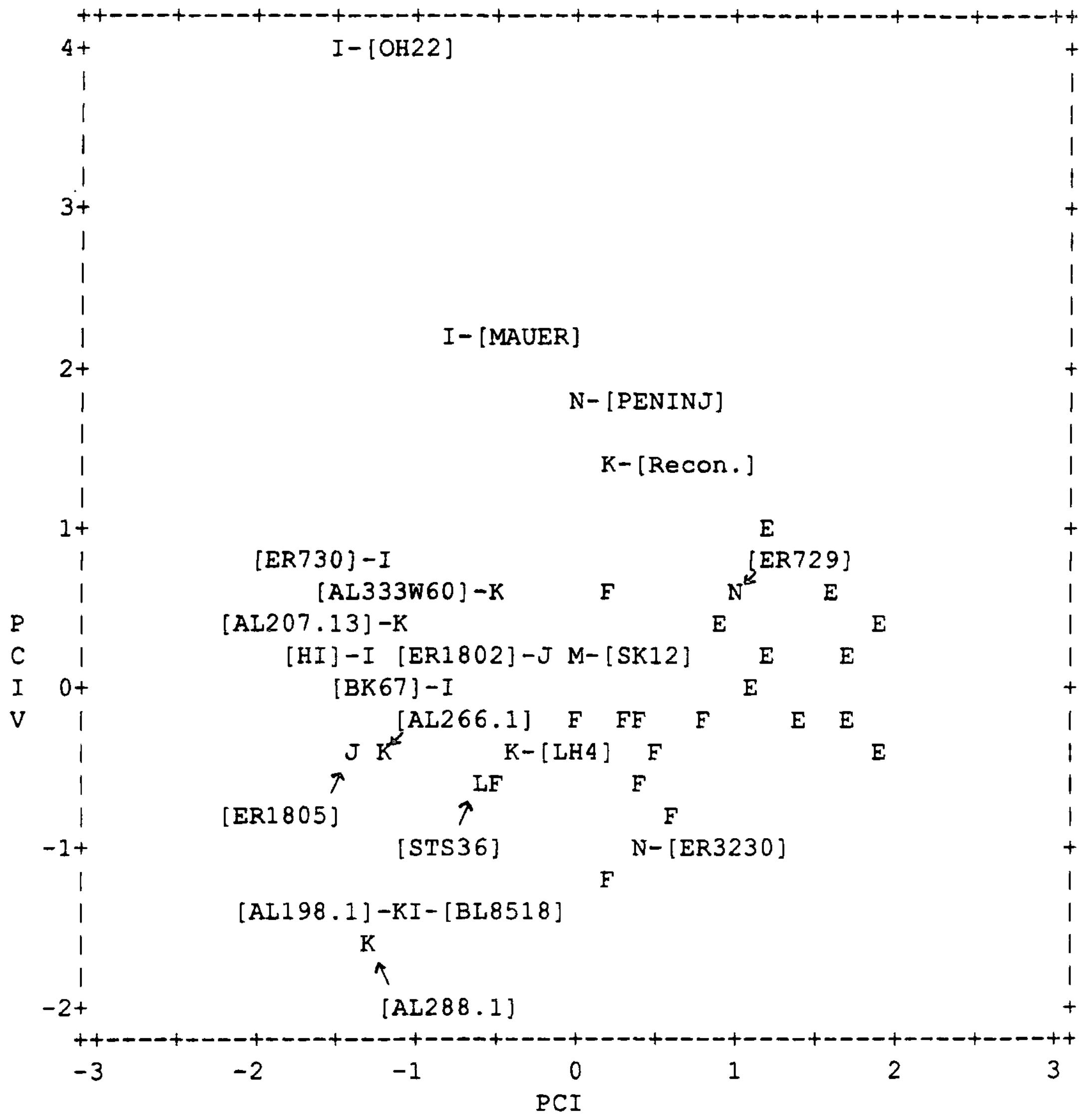
On axis IV, the range of scores for *H. erectus*, *A. boisei*, and *A. afarensis* exceeds that for the *Gorilla* sexes combined (see figure 6.01C). For *H. erectus*, only if OH 22 and Mauer are excluded is the range similar to that of *Gorilla* (sexes combined). The value of M2 on OH 22 is estimated. I reexamined this specimen and believe that I have overestimated its value for this measurement (6.6cm). I reestimated the value of M2 for OH 22 and changed the value entered in the database to the new estimate (5.0). This was done for the purpose of the canonical variates analysis discussed in the second half of this chapter which requires low within-group variability. Of the remaining specimens, the distance between the scores of BL 8518 and Mauer indicate that they both cannot belong to a group containing KNM-ER 730 and BK 67.

FIGURE 6.01B: MANDIBLE: PLOT OF PCIII WITH PCI

```
       ++----+----+----+----+----+----+----+----+----+----+----+----++
      3+                                                             +
       |                                                             |
       |                                  N-[ER3230]                 |
       |                                                             |
       |                                                             |
      2+                                        N-[ER729]            +
       |           [ER730]                                           |
       |                 ↘            M-[SK12]                       |
       |                  I     L-[STS36]                            |
       |                      I-[MAUER]                              |
      1+                                                             +
       |                                          E                  |
       |         [AL198.1]-KI-[BL8518]    F            E             |
   P   |                     [PENINJ]-N F      E    E    E           |
   C   |                 [ER1805]        F    F       E  E           |
   I  0+                 ↙            F                              +
   I   |        [OH22]-IJI-[HI]         F F            E             |
   I   |                  ↗K     K-LH4                               |
       |        [AL207.13]       F                                   |
       |               [BK67]-I     J-[ER1802]   E                   |
     -1+       [AL288.1]-KK-[AL266.1]                                +
       |                                  FF                         |
       |                                                             |
       |                                K         E                  |
       |              [AL333W60]-K       ↖                           |
     -2+                                 [Recon.]                    +
       ++----+----+----+----+----+----+----+----+----+----+----+----++
       -3        -2        -1         0         1         2         3
                                    PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

FIGURE 6.01C: MANDIBLE: PLOT OF PCIV WITH PCI



E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

The value of M2 is estimated on KNM-ER 3230 so the range of scores may be less for *A. boisei.* If the reconstructed mandible is excluded then the range of scores for *A. afarensis* would be approximately equal to that for *Gorilla* (sexes combined). The *H. habilis* specimens are not widely separated on this axis. The *A. africanus* specimen has a PC score closest to that of LH 4 and a female *Gorilla* while the *A. robustus* specimen has a score close to that of KNM-ER 1802.

Overall, *H. erectus* crania cluster close together on PC axes I and II but the scores are more spread out on axis III and IV. OH 22 and HI are probably females on the basis of size while Mauer and BK 67 are likely to be males. BL 8518 and KNM-ER 730 could be of either sex. Of the *H. habilis* specimens, KNM-ER 1805 has a small score on axis I and KNM-ER 1802 a large one but they have close scores for axes II, III, and IV. These two specimens are probably both males but KNM-ER 1805 may be affected by pathology. STS 36 is smaller than any of the robust australopithecines and while its score falls within the *A. boisei* range on axis III, on axis IV its score is close to LH 4, A. L. 266.1, KNM-ER 1805 and 3230. This may be a male *A. africanus.* SK12 falls within the *A. boisei* range on all PC's and it is doubtless a male *A. robustus.* Within the *A. boisei* sample, Peninj has the smallest score on axis I and KNM-ER 729 the largest. The three specimens group together most closely on axis I and II, whereas on axis III and IV they are more widely separated. On axis III, KNM-ER 3230 and 729 have the closest scores but on axis IV Peninj and KNM-ER 729 are closer. All three specimens are likely to be male. On axis I A. L. 288.1, 207.13, 266.1, and 198.1 have small scores and A. L. 333w.60, LH 4, and the reconstructed mandible have larger scores. On axes II, III, and IV, the range of *A. afarensis* is greater than that found in *Gorilla*, an indication that the sample is heterogeneous.

6.2.2 Palate

Six palatal measurements are used in this PCA since this results in 16 fossil hominids being plotted (P1- total length; P2- internal alveolar length; P3- alveolar length; P4- external alveolar breadth; P7- depth at M1; P9- bicanine breadth). If all nine palatal variables are used, only 11 fossil individuals can be included. See Appendix 4A for tables of correlation and rotated PC matrices.

The first three PC's account for 94.1 % of the total sample variance with PCI accounting for 67 %, PCII 17.8 %, and PCIII 9.3 % of that variance. The variables with the highest loadings on PCI are P1 (length), P3 (alveolar length), and P9 (bicanine breadth) and all loadings are positive. The axis thus describes overall dimensions of the palate and so would be expected to distinguish large from small individuals. On PCII the highest loadings are on P4 (external breadth) and P2 (internal alveolar breadth) and all loadings are positive. This PC could be expected to distinguish between individuals with narrow versus wide teeth and/ or narrow versus wide palates. P7 (depth at M1) is the only variable with a high loading on PCIII but all variables have positive loadings.

For PCI the range of PC scores for *Gorilla* males far exceeds that of the females (see figure 6.02A). All males are positioned in the right half of the plot and most male scores exceed those of the females.

Sangiran 17 is located in the upper left quadrant and its score falls within the range of *A. robustus*, *A. boisei*, and *H. habilis.* The ranges of scores for the species of *H. habilis*, *A. robustus*, and *A. africanus* are smaller than those for *Gorilla* females and those of *A. boisei* and *A. afarensis* are less than those of *Gorilla* males. Overall PCI seems to separate the hominids from the pongids.

The ranges of scores for *Gorilla* males and females on axis II are of approximately the same size and are overlapping (see figure 6.02A). Sangiran 17 has the highest score of all hominids on this axis, OH 24 and KNM-ER 1813 have close scores on this axis, and the range of PC scores for *A. afarensis* falls within that of the *Gorilla* sexes. *A. robustus* and *A. boisei* have ranges of scores that are less than either sex of *Gorilla* and the scores of both groups overlap on axis I and II. The range of scores of *A. africanus* exceeds that of both sexes of *Gorilla* but not the species range. If STS 5 is female then STS 53 and STS 52 should not be the same sex as each other but STS 52 is not fully mature and so it may be an immature individual of either sex. If this latter specimen's immaturity is what is causing its low score then all four specimens could be females. However, if the scores of the *A. africanus* specimens follow the pattern of the *Gorilla* sexes, then STS 5 and STS 53 should be males and STW 73 and possibly STS 52 females.

The PC scores for both sexes of *Gorilla* almost totally overlap on PCIII with females being more variable than males. Therefore this axis is not discriminating on the basis of sex. The fossil hominids are less variable along this axis than *Gorilla* with *A. africanus* the most variable group. *A. africanus* has the same size of range as *Gorilla* males but falls within the range of the *Gorilla* species (see figure 6.02B). On the plot of PCIII by I, the scores of *Gorilla* almost totally overlap those of the fossils. Members of *A. boisei* have the highest scores, then *A. robustus* and *H. habilis*, with *A. afarensis* having the lowest scores of the hominids while the scores of *A. africanus*

FIGURE 6.02A: PALATE: PLOT OF PCII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+----++
  3+                                                             +
   |                                                             |
   |                                                             |
   |                    I-[SANGIRAN17]                           |
   |                                                             |
  2+                                                             +
   |                       M-[SK83]                              |
   |                                                             |
   |                   N-[ER405]                                 |
   |                                                     E       |
  1+                                                             +
   |       [ER406]-N                             E               |
   |                        N-[OH5]       E      E               |
P  |          [SK79]-M                    E                      |
C  |                            [AL200.1] F FF     E E           |
I 0+         [ER1813]-J   M-[SK48] ↓  F                          +
I  |                 [STS53]-L     K    F                        |
   |                 [STS5]-L      K E          E                |
   |               [OH24]-J       ↑    F                         |
   |                         [Recon.] F                          |
 -1+                                 F                           +
   |          [AL199.1]-K                                        |
   |                                   F   F                     |
   |                          L-[STW73]                          |
   |                                                             |
 -2+                      L-[STS52]                              +
   ++----+----+----+----+----+----+----+----+----+----+----+----++
   -3        -2        -1         0         1         2         3
                                 PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

FIGURE 6.02B: PALATE: PLOT OF PCIII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+----++
  2+                          [OH5]                              +
   |                         ↑                                   |
   |       [ER406]-N        N         F F E                      |
   |                                                             |
   |                      L-[STS52]                              |
  1+           [ER405]-N             E                           +
   |                                 F                           |
   |          [SK79]-M      L-[STS5]      E        E E           |
P  |                                       F     E               |
C  |                      M-[SK48]    FF                         |
I 0+         [ER1813]-J   J-[OH24]              E                +
I  |                       M-[SK83]    F                 E       |
I  |      [SANGIRAN17]-IK-[AL199.1]       F F                    |
   |                          L-[STS53]                          |
   |                                             E               |
 -1+                                                             +
   |                                         F                   |
   |                 [STW73]-L                                   |
   |                               K-[AL200.1]                   |
   |                               K-[Recon.]                    |
 -2+                                                             +
   ++----+----+----+----+----+----+----+----+----+----+----+----++
   -3        -2        -1         0         1         2         3
                                 PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

overlap those of all these groups.

Overall, Sangiran 17 is differentiated from the other fossil hominids on PCII but has a similar score to A. L. 199.1 on PCI and III. KNM-ER 1813 and OH 24 have similar scores on all PC's indicating that they could belong to the same species and possibly the same sex. The *A. africanus* specimens are most similar on axis I but on axes II and III have a wider spread of scores. The four *A. africanus* specimens may be females (since STS 52 is immature) or else STS 5 and STS 53 are males and the other two specimens, females. Of the *A. afarensis* specimens, A. L. 200.1 and the reconstructed palate are separated from A. L. 199.1 on all 3 axes indicating that the former two are males and the latter a female of the same group. SK 48 and SK 83 have close scores on axis I and III but SK 48 and 79 have closer scores on axis II. These specimens are probably a combination of males(s) and females(s) but all are likely to belong to the same species. SK 48 is probably a female due to its relatively small palate and cheek teeth while the other two specimens could be males. The three *A. boisei* specimens are close on all three axes and are all males of the same species.

6.2.3 Base

The use of 11 characters of the Base region allows the relationships between sixteen fossil hominids to be examined (B3- tympanic width; B4- bistylomastoid width; B5- bistyloid width; B6- bicarotid canal width; B7- apex to apex of petrous temporal; B8- biforamen ovale width; B9- biinfratemporal fossa width; B10- tympanic - carotid canal; B11- carotid canal - apex of petrous temporal; B12- biinfratemporal line - bitympanic line; B13- biforamen ovale line - bitympanic line). See Appendix 4A for tables of correlation and rotated PC matrices.

The first three PC's account for 84.7 % of the total sample variance. PC I accounts for 51.2 %, PCII 27.2 %, and PCIII 6.3 % of the variance. Although the first four PC's account for 88.9 % of the total variance, PCIV only accounts for 4.2 % of it. The variable with the highest loading on PCIV is B11 (carotid canal - apex of petrous temporal) and a plot of PCIV by PCI does not distinguish the hominids from the pongids or the sexes of *Gorilla* from each other and so will not be discussed further.

The variables with the highest loadings on PCI are B3 (bitympanic width), B10 (tympanic - carotid canal), B11 (carotid canal - apex of petrous temporal), B12 (distance between biinfratemporal fossa line to bitympanic line), and B13 (distance between biforamen ovale line to bitympanic line).

B4 (bistylomastoid width), B5 (bistyloid width), B6 (bicarotid canal width), B7 (apex to apex of the petrous temporal), and B9 (biinfratemporal fossa width) all have high loadings on PCII and represent the width of the midline basal structures.

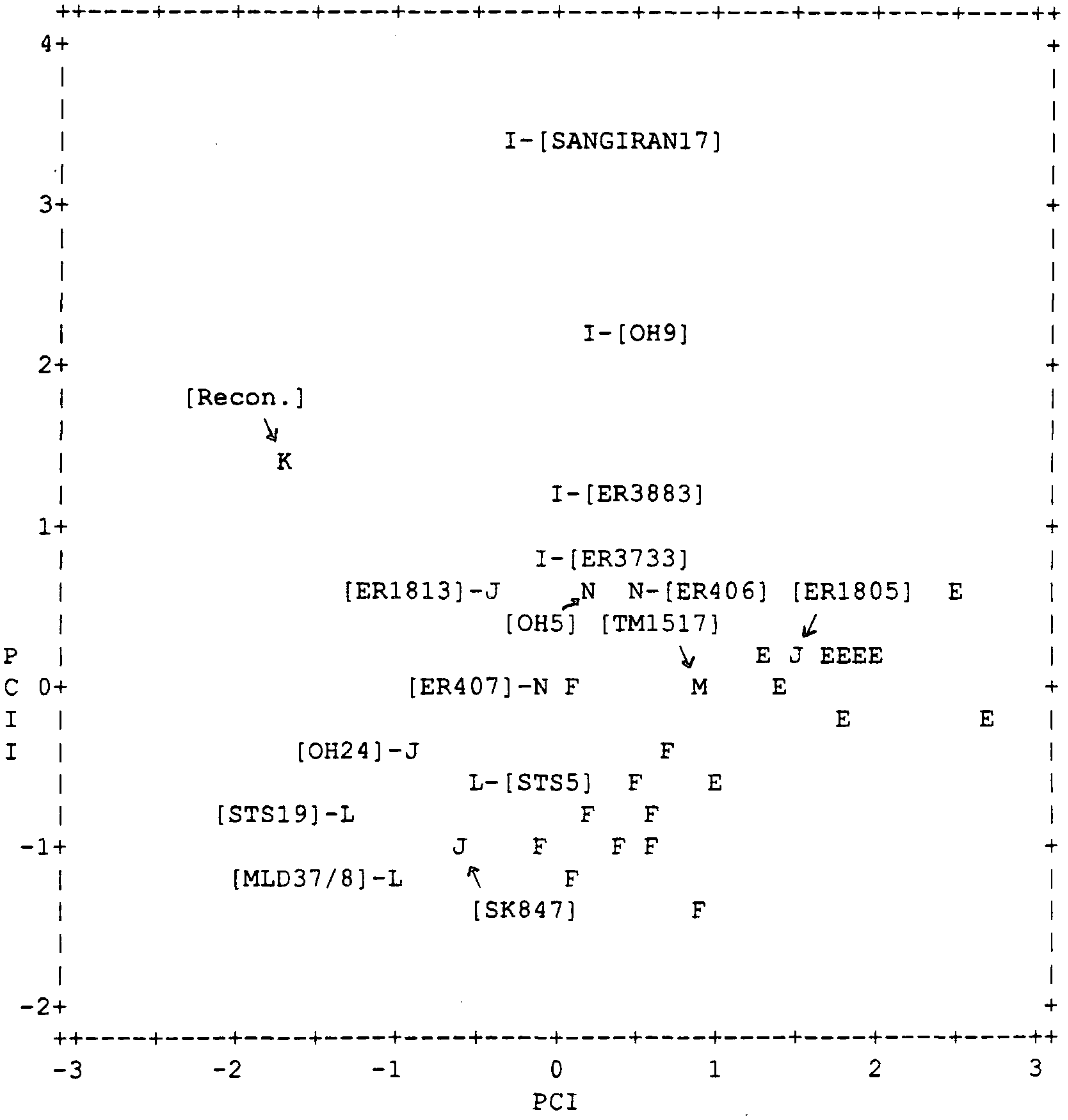
The variables with the highest loadings on PCIII are B7 (apex to apex of the petrous temporal) and B8 (biforamen ovale width) which also represent the width of midline structures, but of the anterior base only.

On axis I, *Gorilla* males have a wider range of scores than females but the ranges of the two sexes do not overlap (see figure 6.03A). The *H. erectus* specimens are all located in the upper left quadrant and their range of scores is much smaller than for either sex of *Gorilla*. OH9 has the largest and Sangiran 17 the lowest score on this axis. The range of scores for *H. habilis* is quite large, greater than the range of male and female *Gorilla* separately, but smaller than the range of *Gorilla* (sexes combined). OH24, KNM-ER 1813, and SK 847 have close scores but KNM-ER 1805 has a much larger score. The reconstructed *A. afarensis* specimen has the lowest score of all the specimens on this axis having smaller values for many of the variables high on PCI. The three *A. africanus* specimens have a range of scores smaller than that of *Gorilla* females with STS 19 having the lowest and STS 5 the highest of these scores. One reason for the position of STS 5 is its greater prognathism relative to other *A. africanus* specimens, which requires a longer anterior basal region. TM 1517 has a longer, wider, anterior base than most of the other hominids and has a score on axis I which falls midway between those of male and female *Gorilla*. The *A. boisei* specimens have a small range of scores and are positioned within the range of scores for *Gorilla* females.

The range of PC scores of male and female *Gorilla* are almost equal on PCII, with some overlap of values (see figure 6.03A). The range of the *H. erectus* specimens, on this axis, is larger than that of *Gorilla* (sexes combined) with KNM-ER 3733 and Sangiran 17 having the lowest and highest scores. The measurement values of Sangiran 17 for most of the variables are larger than those of other specimens but many of them are estimates. If correct, however, they may indicate regional differences between African and Asian *H. erectus*. Otherwise the degree of sexual dimorphism in these variables is greater in *H. erectus* than in *Gorilla*. *H. erectus* crania have the highest scores on this axis than any other specimens (except the *A. afarensis* reconstruction).

The *H. habilis* range of scores exceeds that of either sex of *Gorilla* but not that of the species, suggesting that SK 847 and KNM-ER 1813 cannot be of the same sex. The reconstructed *A. afarensis* specimen is positioned within the *H. erectus* range

FIGURE 6.03A: BASE: PLOT OF PCII WITH PCI



E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

having similar measurement values for B4 - B7 and B9. *A. africanus* specimens have a small range of scores which may indicate that they are all of the same sex. The *A. robustus* specimen is positioned within the male *Gorilla* range and falls just outside the range of *A. boisei*. It also lies within the range of *H. habilis*. *A. boisei* specimens have a small range of scores on this axis with OH 5 and KNM-ER 406 having larger scores than KNM-ER 407.

Of the hominids, *A. africanus* specimens have amongst the lowest, *A. afarensis* and *H. erectus* the highest scores on this axis, the remaining hominids having intermediate scores; that is from narrow to wide mid-basal structures. This axis represents the *H. habilis* and *H. erectus* brain expansion relative to the other hominids but also the need of *A. boisei*, *A. robustus*, and *A. afarensis* for a wider base due to their larger mandibles.

On axis III, mid-basal structures of the anterior part of the base are causing most of the variability (see figure 6.03B). The ranges of scores for male and female *Gorilla* are approximately equal with females having a slightly larger range but the scores of both sexes overlapping completely. *H. erectus*, *A. africanus*, and *A. boisei* all have ranges of scores smaller than either sex of *Gorilla* with most of the specimens having scores within, or just outside, the *Gorilla* range (STS 5, OH 9, KNM-ER 407 having smaller scores than any *Gorilla* specimen). The *A. afarensis* specimen is positioned just outside the *H. erectus* range but within that of *Gorilla*. The *H. habilis* range exceeds that of *Gorilla* and TM 1517 falls within this range with KNM-ER 1813, 1805, and TM 1517 having smaller scores on this axis than any other hominid. KNM-ER 1813 has a smaller measurement value for B8 than the other hominids but this value was estimated. TM 1517 has estimated values for B7 and B8, and for KNM-ER 1805, B7 and B13 are estimated. Thus these specimens may be more similar to the other hominoids than figure 6.03B would seem to indicate.

The overall assessment of each PC shows the *Gorilla* sexes to be totally separate on axis I, slightly on axis II, and not at all on axis III. *H. erectus* are close on axis I but axis II may indicate differences between African and Asian specimens of *H. erectus* with Sangiran 17 having a larger cranial capacity and therefore a need for a wider base than the African specimens. On axis III the *H. erectus* range does not exceed that of *Gorilla* but KNM-ER 3733 (supposed female) and Sangiran 17 (possible male) have close values as do KNM-ER 3883 (supposed male) and OH 9 (possible male). Thus *H. erectus* are not very dimorphic for B7 and B8.

KNM-ER 1813, OH 24, and SK 847 are close in figure 6.03A but KNM-ER 1805 is

FIGURE 6.03B: BASE: PLOT OF PCIII WITH PCI

```
    ++----+----+----+----+----+----+----+----+----+----+----+----++
   2+                                                             +
    |                                                             |
    |                                                             |
    |       [Recon.]        [ER3733]F                             |
    |            ↘               ↘       F   E        E           |
   1+             K[SANGIRAN17]-I IFF                  E          +
    |                                    F      E                 |
    |                                  F                          |
 P  |                                N-[OH5]F               E     |
 C  |          [MLD37/8]-LJ-[OH24]      F[ER406]     E            |
 I 0+                                    ↙                        +
 I  |         [STS19]-L   [ER3883]-I    N F      E                |
 I  |                                F              EE        E   |
    |                  [STS5]-L      I-[OH9]                      |
    |                [SK847]-J                                    |
  -1+                             N-[ER407]                       +
    |                                                             |
    |                                                             |
    |                                                             |
    |                                       M-[TM1517]            |
  -2+                                                             +
    |                                             J-[ER1805]      |
    |                                                             |
    |                          J-[ER1813]                         |
    |                                                             |
  -3+                                                             +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
    -3        -2        -1         0         1         2         3
                                  PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

far removed. The situation for PCI is very interesting. KNM-ER 1813, OH 24, and SK 847 have PC scores intermediate between *A. afarensis* and *H. erectus* while KNM-ER 1805 has the highest score of all the hominids. On PCI five measurements have high loadings, two of which include: B12 (biinfratemporal line - bitympanic line) and B13 (biforamen ovale line - bitympanic line). A check of the original measurements shows that my values are identical to those of Dean and Wood (1982) for these variables. I decided to make a comparison of the values of KNM-ER 1805 with those of the other hominids and modern hominoids by taking the ratio of the two measurements (B12:B13). The ratio for modern humans is 1: .56 for both sexes. Of the hominoids, the values of the *Pongo* sexes are the smallest (1: .5 for both sexes) and *Gorilla* has the largest values (1: .6) for both sexes. The values of the majority of fossil hominids lie between .5 and .61. The exceptions are STS 25, KNM-ER 407, KNM-ER 1470, SK 847, SANGIRAN 17, and KNM-ER 1805.

For STS 25 my measurements give a ratio of 1: .71, those of Dean and Wood (1982) 1: .86, but when checked against the diagram in Dean and Wood (1982) give a ratio of 1 : 52. My measurement of B13 for KNM-ER 407, taken from the left side, gives a ratio of 1 : .74, but using the right side for this measurement gives a value of .53 which is closer to the ratio derived from the diagram in Dean and Wood (1982) (1:.50). For KNM-ER 1470 the ratio is 1 : .44 using my measurements but if the values of B12 and B13 obtained by Dean and Wood (1982) are used the ratio for KNM-ER 1470 is 1 : .48. SK 847 has a ratio of 1 : .64 and SANGIRAN 17 1 : .44 but I have not checked these measurements against casts as yet. However, the ratio obtained for KNM-ER 1805 is 1: .7. As mentioned before, I checked the original values which correspond to those of Dean and Wood (1982), then I reexamined a cast of the specimen and obtained similar values, and finally I measured the diagram in the Dean and Wood (1982) article (40 % of original size) and still I obtained the ratio 1: .7.

Dean and Wood (1982) show the similarities between KNM-ER 1805 and the 'robust' australopithecines. White, Johanson, and Kimbel (1981:456) describe KNM-ER 1805 as having a "bizarre morphological configuration" and state that "the large size incongruity between major constituents of the skull plus its persistent metopic suture suggest the possibility of some growth abnormality". I can only conclude that either the position of the foramen ovale 1) has been mislocated by myself and others; or 2) KNM-ER 1805 has cranial base morphology unlike both modern *H. sapiens* and the extant hominoids as well as the fossil hominids measured (see also section 6.2.1).

The reconstructed cranium has the smallest score on PCI. It lies within the *H.*

erectus range on PCII and within the pongid range on PCIII. Thus it is shorter in length (B13) and smaller in width (B3) but wider in the mid-line structures which isolates from the other hominids in figures 6.03A and B. STS 5, STS 19, and MLD 37/38 are close on all three axes which may indicate that they are all females. TM 1517 falls within the *Gorilla* range on axes I and II but for PCII it also has values similar to KNM-ER 407 and 1805 and on axis III it is closest to KNM-ER 1805 and is possibly a female. All three *A. boisei* specimens are close on axes I and II but are more widely spread on axis III. There is thus no reason to doubt that they all belong to the same species and are males.

6.2.4 Vault

The use of eight variables allows sixteen fossil hominids to be analysed (V1- frontal breadth; V3- frontal arc; V4- frontal chord; V5- parietal arc; V6- parietal chord; V10- supraglabellare - bregma chord; V11- inion chord; V12- inion arc). The first three PC's accounted for 91.4 % of the total sample variance. PCI accounts for 58.8 %, PCII 21.0 %, and PCIII 11.5 % of the total sample variance. See Appendix 4A for tables of correlation and rotated PC matrices.

The variables with the highest loadings on PCI are V1 (frontal breadth), V3 (frontal arc), V4 (frontal chord), and V10 (supraglabellar - bregmatic chord). Thus this PC should separate small-brained individuals from larger brained ones, but may not distinguish between specimens with high foreheads from those with a large supraorbital torus.

On PCII, V5 (parietal arc) and V6 (parietal chord) have the largest loadings but V12 (inion arc) has a small negative loading. This axis should separate larger from smaller skulls or individuals with longer from those with shorter parietals.

On PCIII, V11 (inion chord) and V12 (inion arc) have the largest loadings of all the variables on this axis and they relate to the sagittal development of the nuchal area. The position of inion depends on the robusticity of the nuchal muscles with large individuals having inion placed high and small individuals lower down on the occipital bone. This distinguishes between the sexes of some genera (like *Gorilla*) but may also distinguish between specimens with large or small cranial capacities.

On PCI, the scores of the *Gorilla* sexes overlap considerably with only extreme high and low scores separating as males and females respectively. (see figure 6.04A). The range of scores is very large and almost totally overlaps those of the fossil specimens. This is due to an extreme score of one female (1939.914) *Gorilla*. This specimen has the smallest measurement values for V3 and V4 (frontal arc and chord) and

FIGURE 6.04A: VAULT: PLOT OF PCII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+-----++
  3+                                          I-[SANGIRAN17]     +
   |                                                             |
   |                                                             |
   |                                                             |
   |                                                             |
  2+                                                             +
   |                                [OH9]-I          I-[SKULLI]  |
   |                                                             |
   |                                                             |
   |               F                                             |
  1+                                               [SKULLII]     +
   |                                 E      [PITHI]              |
   |                   [STS5]-L   [OH5]-N          I  I [SKULL3] |
P  |                        [OH16]-J N-[ER406]          I        |
C  |                                FJ     I-[ER3883]            |
I 0+                              E[ER1470]  I-[ER3733]   I      +
I  |                                 F                 [SKULLIII]|
   |           [STS71]-L             F    F                      |
   |                            F  F    E    E E                 |
   |                  [ER1813]-J     F                           |
 -1+                                  E                          +
   |                                      E  F                   |
   |                                 E                           |
   |                                              E   E          |
   |                                                             |
 -2+                                                             +
   |                                        F                    |
   |                                                             |
   |                                                             |
   |                                                             |
   |                                                             |
 -3+                                                             +
   ++----+----+----+----+----+----+----+----+----+----+----+-----++
        -3        -2        -1         0         1         2
                                      PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

amongst the highest values for V5 and V6. If bregma was located incorrectly on this specimen, then the range of female *Gorilla* scores on PCI should be much smaller, smaller than that of *Gorilla* males. In either case, the range of scores of all the fossil groups do not exceed the *Gorilla* range of scores on this axis (sexes combined).

The nine *H. erectus* specimens are located in the upper right quadrant of the plot. This axis does not seem to be separating this group by sex (since KNM-ER 3883 and 3733 are presumed male and female). Instead there is some separation of the African from the Asian specimens with the latter group having the higher PC scores. Thus there is some evidence of increased robusticity between KNM-ER 3733 and 3883 on the one hand, and OH 9 and the Asian specimens on the other. The range of Asian *H. erectus* is less than that of *Gorilla* males, but greater than that of *Gorilla* females only if 1939.914 is excluded. Thus this sample probably contains a combination of male and female specimens.

The range of PC scores for *H. habilis* is smaller than that of either sex of *Gorilla*, but the smaller cranial capacity of KNM-ER 1813 (510cc; Holloway 1983) indicates that it is a female (KNM-ER 1470: 752cc; OH 16: 650cc - Holloway 1983).

Only two specimens of *A. africanus* could be included: STS 5 and STS 71. The range of their PC scores is less than that of either sex of *Gorilla* and larger than that of *H. habilis.* These specimens have the lowest PC scores of all the hominoids (except for *Gorilla* female 1939.914) and are probably both females.

The two *A. boisei* specimens have close scores on axis I and are presumed to both be males.

The range of PC scores for *Gorilla* males and females is large on axis II and overlaps most of the fossil PC scores (see figure 6.04A). There are two female *Gorilla* with the highest (1939.914) and lowest (1939.933) scores of the *Gorilla* specimens. If this is due to measurement error then male *Gorilla* would have a wider range of scores than females on PCII.

Of the *H. erectus* specimens, Sangiran 17 has the highest PC score on axis II but V5 and V6 are estimated on this specimen. Sangiran 17, OH9, and Skull I have the highest PC scores and are separate from the other *H. erectus* specimens, as well as the other hominoid specimens, on this axis. Individuals are not being separated on the basis of sex since KNM-ER 3733 and 3883 have similar scores, so perhaps this PC is discriminating on the basis of both cranial capacity and length of the parietal bones.

KNM-ER 1813 has a lower score on axis II than KNM-ER 1470 and OH 16, possibly due to its smaller cranial capacity. STS 5 has a larger cranial capacity than STS 71 and this accounts for their separation on this axis. KNM-ER 406 and OH 5 have close scores on this axis and similar cranial capacities. None of the above fossil groups has a larger range of scores than either of the *Gorilla* sexes.

The male *Gorilla* range on axis III is larger than that of *Gorilla* females and male scores are almost all larger than those of the females. *Gorilla* females have amongst the lowest scores on this plot (see figure 6.04B). Thus this axis discriminates between the *Gorilla* sexes, that is, between individuals having larger or smaller mandibles (requiring greater or lesser sagittal development of the nuchal area).

The range of *H. erectus* scores is approximately equal to that of *Gorilla* males. The plot of PCIII by PCI shows some separation of African and Asian specimens. The earlier African specimens are slightly more robust than the later ones and may have had relatively more robust mandibles. These specimens are not separating on the basis of size of cranial capacity since Pithecanthropus I and KNM-ER 3733, which have small cranial capacities for *H. erectus*, are widely separated on axis III. Instead, separation occurs between individuals with large measurement values for V11 and 12 (KNM-ER 3733 and 3883) and those with small measurement values for these variables (Sangiran 17 and Pithecanthropus I). Thus the location of inion is partially responsible for the separation within this group and the sex or size of the fossils is not the prime discriminant.

The range of scores of *H. habilis* is smaller than that of *Gorilla* males but greater than that of *Gorilla* females. KNM-ER 1470 and 1813 have closer scores to one another than either does to OH 16 due to low estimated values of V11 and 12 for OH 16. KNM-ER 406 and OH 5 have similar scores on this axis. STS 71 has a larger score than STS 5 but the distance between them is less than that between the most extreme *Gorilla* females and so they are probably both females.

Overall, *H. erectus* crania have the largest range of scores on PCI, II, and III. There is no reason to doubt the homogeneity of the sample but it is difficult to determine the sex of individual specimens. Also, there is some indication of either regional or temporal differences between the African and Asian specimens. The three *H. habilis* specimens could belong to one group but although KNM-ER 1470 and 1813 may represent a male and female, OH 16 could be of either sex. The *A. boisei* specimens are presumably both males and the *A. africanus* specimens both females.

FIGURE 6.04B: VAULT: PLOT OF PCIII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+----++
  3+                                                             +
   |                                                             |
   |                                                             |
   |                                                             |
   |                          J-[ER1813]                         |
  2+                                                             +
   |                             [ER3883]-I I-[ER3733]           |
   |          [STS71]-L             J-[ER1470]                   |
   |                                                             |
   |                                E                            |
  1+                             E       I-[OH9]                 +
   |                  [STS5]-L         E      [SKULLIII]-I       |
P  |                                             E               |
C  |                                          E    [SKULLI]      |
I  |                                     E          I            |
I 0+                       [OH16]-J     [OH5]         I-[SKULLII]+
I  |                        [ER406]-NE N    E           I        |
   |                                                   [SKULL3]  |
   |                            [SANGIRAN17]-I    I-[PITHI]      |
   |                              F        F                     |
 -1+                           F                     E           +
   |              F                 E                            |
   |                                F       F                    |
   |                                F                            |
   |                               FF                            |
 -2+                                     F                       +
   ++----+----+----+----+----+----+----+----+----+----+----+----++
        -3        -2        -1         0         1         2
                                      PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

6.2.5 Face

Using twelve measurements of the face allows 13 specimens of fossil hominids to be entered into a PCA (F1- biorbital breadth; F2- interorbital breadth; F3- maximum orbit breadth; F4- orbit height; F8- upper facial breadth; F9- bimaxillary chord; F10- zygomaxillary subtense; F11- subspinale - zygomaxillary chord; F12- facial height; F13- nasal height; F21- cheek height; F23- lateral facial length). The first three PC's account for 89.2 % of the total sample variance. PCI accounts for 72.7 %, PCII 11.1 %, and PCIII 5.4 % of the variance. See Appendix 4A for tables of correlation and rotated PC matrices.

On PCI, the variables with the highest loadings are F1 (biorbital breadth), F3 (maximum orbit breadth), F8 (upper facial breadth), F9 (bimaxillary chord), F11 (subspinale - zygomaxillary chord), F21 (cheek height), and F23 (lateral facial length). Overall this PC describes width and length of the face and thus should separate wide from narrow faces as well as longer from shorter faces.

F4 (orbit height), F10 (zygomaxillary subtense), F12 (facial height), and F13 (nasal height) have the highest loadings on PCII and seem to be describing facial height and projection. This PC should separate longer from shorter faces as well as prognathic from orthognathic faces.

PCIII shows only one variable with a high loading, F2 (interorbital breadth).

All *Gorilla* specimens are located in the upper half of the plot (see figure 6.05A). Males have a much larger range of scores than females due to one male individual (2311296). This individual has a very flat and long face untypical of male *Gorilla* in general. Apart from this specimen, male and female PC scores overlap somewhat on PCI with males generally having higher scores than females.

The distance between Sangiran 17 and KNM-ER 3733 is smaller than that between the extremes of either sex of *Gorilla* with Sangiran 17 falling just within the male *Gorilla* range and KNM-ER 3733 within the female range. If KNM-ER 3733 is female and Sangiran 17 male then the degree of sexual dimorphism is less than that in *Gorilla*, at least for these variables. The range of *H. habilis* exceeds that of *Gorilla* females but is smaller than that for *Gorilla* males (even if 2311296 is excluded). KNM-ER 1813 has one of the lowest scores on this axis along with the reconstructed *A. afarensis* cranium. KNM-ER 1470 has the largest score with OH 24 and SK 847 closer to KNM-ER 1470 than to KNM-ER 1813. The *A. boisei* range of scores is less than that of *Gorilla* with OH 5 and KNM-ER 406 having close scores, larger than that of KNM-ER 732. The distance between STS 5 and 71 is smaller than that between

FIGURE 6.05A: FACE: PLOT OF PCII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+----++
  3+                    E                                        +
   |                                                             |
   |                                                             |
   |                                                             |
   |                                                             |
  2+                                                             +
   |                                                             |
   |                                                             |
   |                   F F        E                              |
   |                                  E                          |
  1+                           F                     E           +
   |                      F F  FF                                |
   |                                       E       E             |
P  |                                F  E        EE               |
C  |                                F  F             E           |
I 0+           [Recon.]                                          +
I  |              ↘                       N-[OH5]                |
   |               K            I-[ER3733]                       |
   |      [ER1813]-J    L-[STS71]    J-[ER1470]                  |
   |                             J-[SK847]                       |
 -1+                                   I-[SANGIRAN17]            +
   |                    [ER732]-NM-[SK48]  N-[ER406]             |
   |                      [OH24]-J  L-[STS5]                     |
   |                                                             |
   |                                                             |
 -2+                                                             +
   ++----+----+----+----+----+----+----+----+----+----+----+----++
   -3        -2        -1          0         1         2         3
                                 PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

the extreme *Gorilla* females. STS 5 is more prognathic (F11) and has a longer face (F23) than STS 71. SK 48 has a PC score close to those of KNM-ER 732 and OH 24.

On axis II, *Gorilla* males have a wider range of scores than females unless 2311962 is excluded, in which case the scores of both sexes are totally overlapping and of equal size. All *Gorilla* scores lie in the upper half of the plot and all hominids in the lower half. None of the hominid groups has a range that exceeds those of either sex of *Gorilla*. Thus PCII seems to be distinguishing between hominids and pongids.

Values of male and female *Gorilla* PC scores overlap on PCIII, but most males are located in the upper right quadrant and females in the lower left quadrant of the plot so there is some separation by sex (see figure 6.05B). The range of *H. erectus* scores is less than that of either sex of *Gorilla*. There is some degree of separation by sex with Sangiran 17 having a score similar to male *Gorilla* and KNM-ER 3733 one closer to *Gorilla* females. The same situation seems to be happening amongst the *H. habilis* specimens with KNM-ER 1470 having a PC score closer to the *Gorilla* males and the other specimens closer to *Gorilla* females (though KNM-ER 1813 has a lower value on PCI). Both *A. africanus* specimens have scores like *Gorilla* females while SK 48 has a score like *Gorilla* males. Separation also occurs within the *A. boisei* sample with OH 5 and KNM-ER 406 in the upper right quadrant and KNM-ER 732 in the lower left quadrant. The *A. afarensis* reconstructed cranium is separated from all the hominoids in this plot which may indicate that it was incorrectly reconstructed for F2 and possibly for some variables on PCII.

Overall, Sangiran 17 is probably male and KNM-ER 3733 a female *H. erectus* and they are similar enough on all three axes to be of the same species. Of the *H. habilis* specimens, KNM-ER 1470 is likely to be a male and the other specimens likely to be females. The *A. africanus* specimens are probably both females and the *A. robustus* specimen a likely female. On PCI and III, OH 5 and KNM-ER 406 have similar scores but not on PCII due to the value of F12 for OH 5. This value of facial length for OH5 is suspect (Williams 1985) since a realignment of its face causes a reduction of facial height. So OH 5 should have a shorter face and a PC score on PCII closer to that of KNM-ER 406. Thus OH 5 and KNM-ER 406 are males and KNM-ER 732 probably a female of the same species. The *A. afarensis* specimen has one of the smallest scores on PCI and on PCII is in the upper range of hominid values meaning that it has a long, narrow face. The interorbital breadth (F2) was probably incorrectly reconstructed since this specimen is well separated from the other hominoids on PCIII.

FIGURE 6.05B: FACE: PLOT OF PCIII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+----++
  3+                                                             +
   |               K-[Recon.]                                    |
   |                                                             |
   |                                                             |
   |                                                             |
  2+                                                             +
   |                                                             |
   |                                                             |
   |                                  E                          |
   |                                   I-[SANGIRAN17]            |
  1+                                   E   E       E             +
   |                              E   [ER1470]                   |
   |                      [SK48]-M    ↙          E               |
P  |                   [ER3733]-I    J     N-[ER406]             |
C  |      [ER1813]-J                                             |
I 0+                   F F                N-[OH5]                +
I  |                    E                            E           |
I  |                           F    F                            |
   |                           F J-[OH24]                        |
   |                                F           E    E           |
 -1+            [STS71]-L F      J-[SK847]                       +
   |                    [ER732]-N   L-[STS5]                     |
   |                           F       F                         |
   |                        F                                    |
   |                                                             |
 -2+                                                             +
   ++----+----+----+----+----+----+----+----+----+----+----+----++
   -3        -2        -1         0         1         2         3
                                 PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

6.2.6 Regional Combination

For this final analysis, variables are chosen to provide a cross-regional assessment and are ones which, in the univariate analysis, proved to be undimorphic and unvariable for modern hominoids (though since *Gorilla* is the most dimorphic of the modern groups some separation by sex should be expected) to assess the homogeneity of the samples. Of these variables, only those which allow the maximum number of fossil specimens to be analysed, with the minimum loss of information, are used. This means that none of the mandibular variables is used since rarely are mandibles and skulls of the same individual found together. Palatal measurements are not used since a combination of measurements from the base, vault, and face allows the largest sample of fossil hominids to be analysed.

The use of seven measurements from these three regions allows the comparison of eleven fossil specimens (B6- bicarotid canal width; B8- biforamen ovale width; B9- biinfratemporal fossa width; V1- frontal breadth; V2- parietal breadth; F1- biorbital breadth; F4- orbit height). The first four PC's account for 92.5 % of the variance. PCI accounts for 50 %, PCII for 24 %, PCIII 10.8 %, and PCIV 7.7 % of the total sample variance. See Appendix 4A for tables of correlation and rotated PC matrices.

V1 and V2 (frontal and parietal breadth) have high loadings on PCI and would be expected to separate large from small brained individuals. On PCII, F1 (biorbital breadth) and F4 (orbit height) have high loadings. B6 (bicarotid canal width) and B9 (biinfratemporal fossa width) have high loadings on PCIII. On PCIV, B8 (biforamen ovale width) has the highest loading.

On axis I, the male *Gorilla* range of scores totally overlaps that of the females of this group with the female range smaller than the male range (see figure 6.06A) The range of PC scores of *H. erectus* exceeds that of *Gorilla* females but not males with Sangiran 17 having the largest and KNM-ER 3883 the smallest PC scores. KNM-ER 3733 has a larger score than KNM-ER 3883 on this axis because its frontal breadth area is slightly more inflated laterally. *H. erectus* is separate from the other species presumably on the basis of greater cranial capacity. Of the *H. habilis* specimens, KNM-ER 1470 has the largest score, intermediate between KNM-ER 3733 and 1813, due to its greater cranial capacity compared to the other *H. habilis* specimens. The range of these specimens is less than that of *Gorilla* females thus there is no reason to doubt the homogeneity of this sample based on these characters. The range of scores of the *A. boisei* specimens is just smaller than that for *Gorilla* males. Although KNM-ER 406 and OH 5 have larger cranial capacities than KNM-ER 732, this latter

FIGURE 6.06A: REGIONAL COMBINATION: PLOT OF PCII WITH PCI

```
   ++----+----+----+----+----+----+----+----+----+----+----+----++
  2+                     E                                       +
   |                                 E                           |
   |                         E                                   |
   |                            E                                |
   |                       E    E                                |
  1+                          E                                  +
   |                            F                                |
   |                E     E   F                                  |
P  |                      F                                      |
C  |                        EF                                   |
I 0+      [ER406]-N         FFF [ER3883]-I       I-[ER3733]      +
I  |                          F                         I        |
   |                         F   F                     ↗         |
   |                  [OH5]-N        J-[ER1470]    [SANGIRAN17]  |
   |                            J-[ER1813]                       |
 -1+         [Recon.]-K                                          +
   |                     [OH24]-JN-[ER732]                       |
   |                          L                                  |
   |                           ↖                                 |
   |                           [STS5]                            |
 -2+                                                             +
   ++----+----+----+----+----+----+----+----+----+----+----+----++
   -3        -2        -1         0         1         2         3
                                 PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

specimen is less constricted post-orbitally for its size than the other specimens. STS 5 has an intermediate score on this axis compared to the other non-erectus hominoids with a score closest in value to OH 24 and KNM-ER 1813. The *A. afarensis* reconstruction has a smaller score relative to the other hominoids with a score intermediate between OH 5 and KNM-ER 406. It is more constricted post-orbitally, but this area is reconstructed.

On PCII, the ranges of male and female *Gorilla* somewhat overlap with males having generally larger scores and with a larger range than females. All three *H. erectus* specimens have very close scores on this axis and fall within the female *Gorilla* range. The range of scores of the *H. habilis* specimens is small with KNM-ER 1470 having the largest and OH 24 the smallest scores. The range of scores for *A. boisei* is similar to that for *Gorilla* females but smaller than that of *Gorilla* males. STS 5 has the smallest score on this axis and is similar to OH 24 and KNM-ER 732 in the size of its orbits. The *A. afarensis* specimen's score falls within the range of *H. habilis* and *A. boisei*. Overall, on this axis there is some separation of hominids from pongids with *A. afarensis*, STS 5, KNM-ER 732, and OH 24 small, KNM-ER 406, *H. erectus*, KNM-ER 1813, KNM-ER 1470, OH 5, and female *Gorilla* intermediate, and male *Gorilla* large.

On PCIII, the scores of male and female *Gorilla* overlap but the male range is slightly larger than the female range with most male specimens having larger PC scores than females (see figure 6.06B). The range of PC scores for *H. erectus* is less than that of either sex of *Gorilla*. Sangiran 17 has the largest and KNM-ER 3733 the smallest scores so this PC may discriminate somewhat on the basis of sex, but probably more on the basis of size since KNM-ER 3883 has a score intermediate between the two specimens and one not close to Sangiran 17. The *H. habilis* range is smaller than that of *Gorilla* males but larger than that of *Gorilla* females due to KNM-ER 1813 and 1470 having wider bases than OH 24. The range of *A. boisei* scores exceeds that of *Gorilla* (sexes combined) but the value of B6 was estimated on KNM-ER 732. STS 5 has a score similar to that of OH 24 while that of the *A. afarensis* specimen is the largest of all the hominoids, closest to KNM-ER 406. The values of B6 and B9 were estimated on this specimen since they fell on reconstructed matrix, not fossil material.

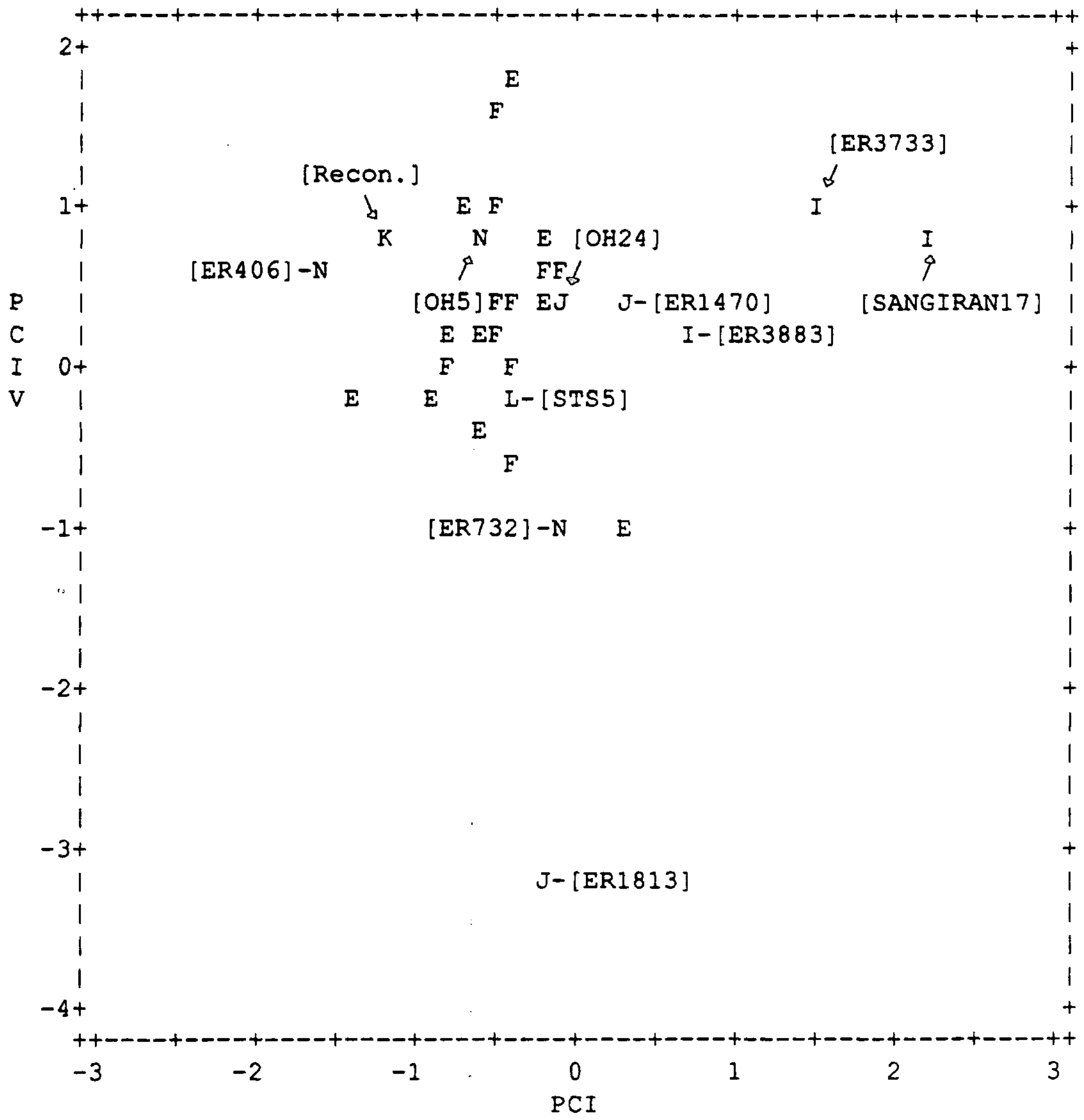
For PCIV, the male *Gorilla* range totally overlaps the female range which is only slightly smaller than the male range. All of the hominid values fall within the *Gorilla* range except that of KNM-ER 1813 for which the value of B8 is estimated. This value causes the wide range of scores for *H. habilis*. The location of the landmarks

FIGURE 6.06B: REGIONAL COMBINATION: PLOT OF PCIII WITH PCI

```
     ++----+----+----+----+----+----+----+----+----+----+----+----++
    3+                                                             +
     |                                                             |
     |                 K-[Recon.]                                  |
     |                                                             |
     |                                                             |
    2+             N-[ER406]                          [SANGIRAN17] +
     |                                                   ↘         |
     |                                                    I        |
     |                           J-[ER1813]                        |
     |                       N-[OH5]                               |
    1+                    EE          J-[ER1470]                   +
     |                      E             I-[ER3883]               |
  P  |                       E                                     |
  C  |                           E    E                            |
  I  |               E         E                                   |
  I 0+                       EF  [STS5]           I-[ER3733]       +
  I  |                        F  ↙                                 |
     |                         FL J-[OH24]                         |
     |                        F                                    |
     |                       FF                                    |
   -1+                     F    EFF                                +
     |                            N-[ER732]                        |
     |                                                             |
     |                         F                                   |
     |                                                             |
   -2+                                                             +
     ++----+----+----+----+----+----+----+----+----+----+----+----++
     -3        -2        -1         0         1         2         3
                                   PCI
```

E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

FIGURE 6.06C: REGIONAL COMBINATION: PLOT OF PCIV WITH PCI



E:GORILLA MALE F: GORILLA FEMALE I: H. ERECTUS J: H. HABILIS
K:A. AFARENSIS L: A. AFRICANUS M: A. ROBUSTUS N: A. BOISEI
$:Multiple occurrence

for this measurement are hard to locate on KNM-ER 1813 and it is likely that I underestimated the value of this measurement. Thus KNM-ER 1813 should have a score closer to those of the other hominoids. *H. erectus* have close scores on this axis. The *A. boisei* range is approximately equal to that of *Gorilla* females with KNM-ER 406 and OH 5 having close scores and KNM-ER 732 having a smaller one. STS 5 falls within the *H. habilis* and *A. boisei* range, intermediate between KNM-ER 3883 and 732, while the *A. afarensis* reconstruction has a score which falls just within the *A. boisei* range.

Overall, PCI separates *H. erectus* from the other hominids. On PCII there is some separation of pongids and hominids, and on PC III and IV scores of both groups overlap. *H. erectus* crania have the closest scores on PCII and IV with some separation on PCIII and most on PCI due to the range of cranial capacities within this sample but the specimens are not so widely separated on any axis that they could not belong to the same species. The *H. habilis* specimens are closest on PCI and II. On PCIII there is some separation and the separation on PCIV is likely due to an under-estimated measurement for KNM-ER 1813. KNM-ER 406 has the smallest score on PCI because it is the most constricted post-orbitally with OH 5 intermediate and KNM-ER 732 having the largest score. On PCII KNM-ER 406 has the largest score, OH 5 is intermediate and KNM-ER 732 the smallest score. KNM-ER 406 and OH 5 have the closest scores on PCIII and IV with that of KNM-ER 732 smaller, probably due to the former two specimens being males and the latter a female. STS 5 is closest overall to OH 24 on all axes and these two specimens are similar in size for most measurements used in this analysis. The reconstructed *A. afarensis* is most similar to *A. boisei* on all four PC's. Some of the measurements for this specimen are close to those of the *A. boisei* values and those measurements that are larger or smaller than those of *A. boisei* are closer to these specimens than to individuals of other species.

6.2.7 Discussion

The PCA allows some discrimination of species by sex, and, in some cases, the groups entered show evidence of heterogeneity. For *H. erectus*, the mandibular region shows some evidence of heterogeneity with Mauer separated on PCIV. The PCA indicates that OH22 and HI are females and Mauer and BK 67 are males, but not necessarily of the same species. In the base, vault, and possibly the regional combination region, there is some evidence of either regional or temporal differences between African and Asian *H. erectus*.

Amongst the *H. habilis* specimens, KNM-ER 1470 is a male as are KNM-ER 1805 and 1802. KNM-ER 1813 and OH 24 are probably both females as indicated by the palate, base, face, and regional combination analyses. In the base analysis, but not in the face analysis, SK 847 appears to be a male while OH 16 could be of either sex. Of all the fossils, only KNM-ER 1805 shows major differences which may be due to pathology.

In the *A. afarensis* mandibular sample, A. L. 288.1, 198.1, and 266.1 are females and A. L. 207.13, 333w.60, and possibly LH4, males. LH4, A. L. 333w.60, and the reconstructed mandible demonstrate differences which may mean this sample is heterogeneous. Of the palate sample, A. L. 200.1 is a male and 199.1 a female of the same species. In the base, face, and regional combination areas only the reconstructed cranium is used.

STS 5 and 71 would seem to be females according to the vault, face, and regional combination analyses while STS 36 is a male *A. africanus*. In the palate analysis, STS 5, 53, 52, and STW 73 could all be females or else the former two are males and the latter two females. In the base analysis STS 5, 19, and MLD 37/38 could all be females. There is no reason to doubt the homogeneity of this sample of fossils.

The SK 12 mandible is a male, SK 48 is female, while SK 83 and 79 are likely males of the species *A. robustus*. TM 1517 is the only *A. robustus* specimen used in the base analysis and may be a female. There is not enough evidence to assess the homogeneity of *A. robustus* as a species, but for the purpose of the CVA all these specimens can be entered as *A. robustus*.

KNM-ER 406, 407, 729, 3230, OH 5, and Peninj are all male *A. boisei* while KNM-ER 732 is a female. All these specimens could belong to one species as the degree of sexual dimorphism does not exceed that of *Gorilla*.

The majority of PC's show these fossils to have ranges equal to or less than those of *Gorilla* males, females, or the species as a whole and in some cases it is possible to discriminate by sex. Homogeneity is most suspect for *H. erectus* and *A. afarensis*. Within *H. erectus* there is some indication that the African and Asian specimens show temporal and/or regional differences (polytypism). Within *A. afarensis* the degree of sexual dimorphism is greater than that found in modern *Gorilla* or else it is possible that A. L. 333w.60 (or the reconstructed cranium) and LH 4 are not *A. afarensis*. This phenomenon cannot be due to regional differences between groups (as in *H. erectus* above) since this would not explain the differences between A. L. 333w.60 and the other Ethiopian specimens. Finally, KNM-ER 1805 shows peculiarities of the basicranial characters which differentiate it from all hominoids.

Since each specimen is entered as a separate entity in the PCA, individual specimen's closeness to/ distance from one another is an indication of their relationship. Using the amount of variability within *Gorilla*, limits can be placed on the amount of acceptable variability within the fossil groups. Sex could be assessed by comparing the pattern of fossil distribution to that of the sexes of *Gorilla*. Thus the PCA has allowed individual sex of fossil specimens as well as the homogeneity of the fossil species to be assessed. These results are used in the second section of this chapter to compare and contrast patterns of variability and sexual dimorphism between fossil and modern groups.

6.3 Introduction

The following Canonical Variate Analyses (CVA) are performed using an SPSSX package on the Durham University mainframe computer (see Chapter 4 for an explanation of the technique). Modern comparators used in these analyses are *H. sapiens*, *Pan*, *Gorilla*, and *Pongo* males and females. Of the fossil groups, no changes are made to the composition of the *A. africanus*, *A. robustus*, and *A. boisei* groups used in the previous (PCA) analyses. Of the *H. erectus* fossils, the African and Asian specimens and the Mauer mandible are entered as separate 'groups'. KNM-ER 1805 is entered separately from the other early *Homo* material. Of the *A. afarensis* material, A. L. 288.1, 198.1, 266.1, and 207.13 are entered as *A. afarensis* while LH 4, and A. L. 333w.60 and the reconstructed cranium, are entered as separate 'groups'.

Each cranial region is examined in a separate CVA as in the previous section of this chapter. Each section includes a discussion of the number of canonical variates (CV's) derived and the proportion of the variance accounted for by each CV. The dispersion of groups along the first three or four axes is analysed and interpreted in terms of the scaled loadings of the original characters on each variate and also to determine to which reference group the fossil specimens most closely resemble. Finally, a discussion is presented of the allocation of individual specimens when reclassified with respect to the original groups.

Matrices of the correlation of each character with each CV can be found in Appendix 4B. Matrices of this relationship for each regional analysis are included in this appendix.

6.4 Results

6.4.1 Mandible

As with the PCA, only eight variables are used to maximise the number of fossil hominids utilised in the analysis (M2, M5, M7-M12). The first three canonical variates (CV's) account for 93.62 % of the total variance. The first CV accounts for 62.44 %, the second 26.13 %, and the third 5.05 % of the total sample variance. All three CV's were highly significant ($p < .01$).

The variables are ordered by the size of their loading on each canonical variate. For canonical variate I (CVI), M2- arcadal length (.81) has a high loading, M7- maximum corpus thickness (.3), M10- depth at M1 (.34), M5- symphyseal height (.35), and M11- depth at M3 (.36) have intermediate loadings, the remaining characters have low loadings, and all but those for M8- internal breadth and M8 (external breadth) are positive.

M7 (.67), M9 (.63), and M10 (.55) have high loadings for CVII, M12 (.3), M5 (.33), M8 (.37), and M11 (.37) have intermediate ones, the remaining characters have low loadings, and all are positive.

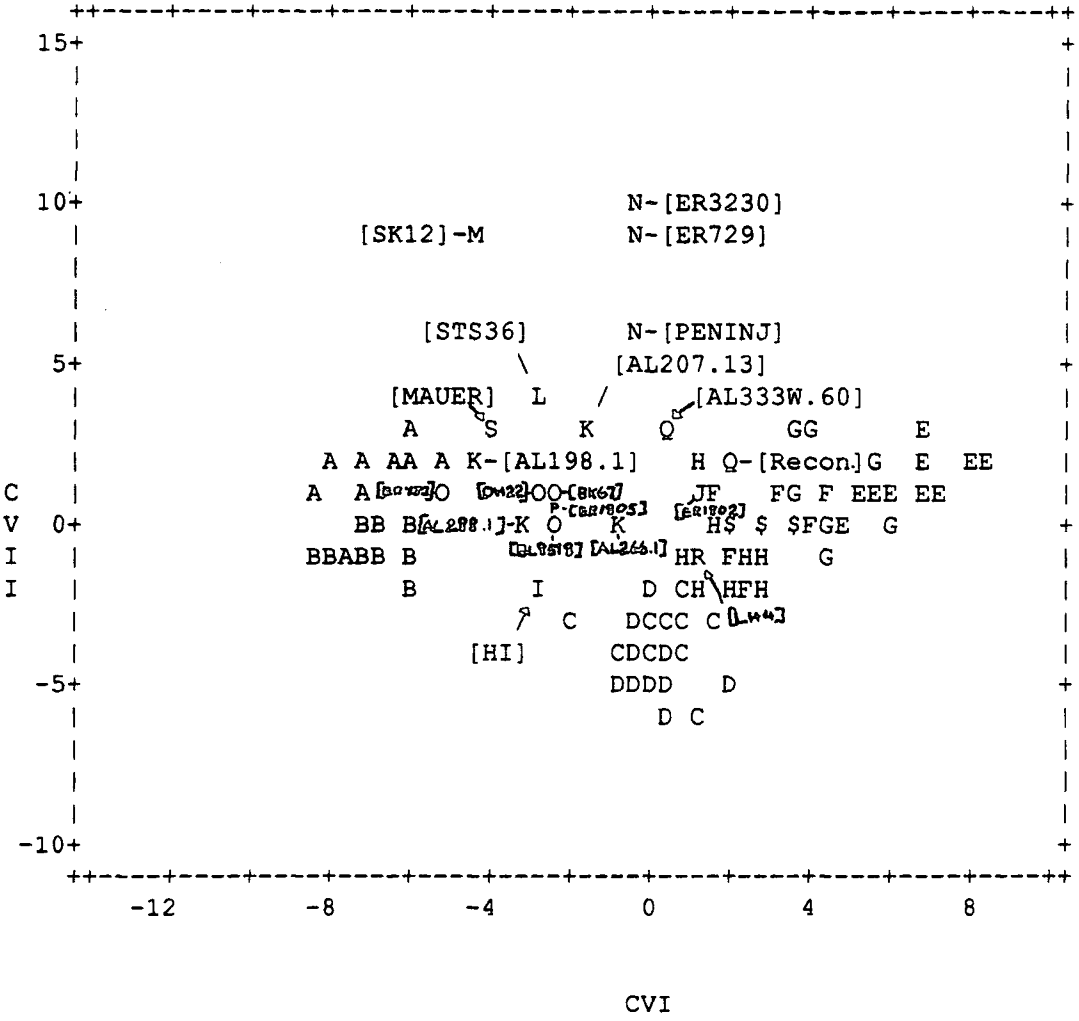
For CVIII, M5 (.51) and M8 (.54) have the highest loadings. The loadings of M7 (-.43), M10 (.31), and M11 (.37) are intermediate, and the remainder have low loadings, one of which is negative.

Figure 6.07A shows the robust australopithecines separated from the other hominoids where they are located in the upper half of the plot. The other groups have scores that are overlapping, with *H. sapiens* in the left half of the plot, pongids in the right half of the plot, and most fossil hominids intermediate between the two. Maximum separation along axis I occurs between *H. sapiens* and the pongids, especially male *Gorilla* and *Pongo*. Of the robust australopithecines, *A. boisei* has a range approximately equal to that of *Pan* males and SK 12 has a high score like the *A. boisei* specimens. STS 36 has a score close that of the Mauer mandible. Of the *A. afarensis* specimens, the range between A. L. 198.1 and the reconstructed mandible is approximately the same as that for both *Gorilla* males and females. LH 4 has a score which falls within the *A. afarensis* range but lies closest to scores of *Pongo* females. The distance between KNM-ER 1802 and 1805 is greater than the separation between extreme male and female *H. sapiens* but less than that between the extreme male and female *Pan*. Of the African *H. erectus* specimens, OH 22, BK 67, and BL 8518 have close scores on axes I and II, while KNM-ER 732 lies within the *H. sapiens* range. The Mauer mandible lies close to the *H. sapiens* scores whereas the Asian *H. erectus* mandible is intermediate between *H. sapiens* and *Pan* with a score on axis I close to the African *H. erectus* specimens.

The order of the groups along axis I corresponds to the overall size of the mandible, and it is probable that this feature is the discriminating factor. The characters which best distinguish these groups are length, thickness, and depth along the corpus. A greater depth along the corpus is related to the size of the cheek teeth and roots, and is also an adaptation to withstand vertical chewing forces generated during mastication (Hylander 1988).

On axis II, the robust australopithecines are separated from the other hominoids. The characters which help to distinguish these groups are external breadth, internal breadth, length, and corpus thickness. Thus it is not only greater size and robusticity

FIGURE 6.07A: MANDIBLE: PLOT OF CVII WITH CVI



A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

of the mandible that is separating these specimens but the greater size of the molars, which require a thicker, deeper corpus.

Figure 6.07B shows a wider separation within groups, than between groups, but with *H. sapiens* dominating the upper left quadrant, the pongids the upper right quadrant, and many of the fossil hominid scores intermediate.

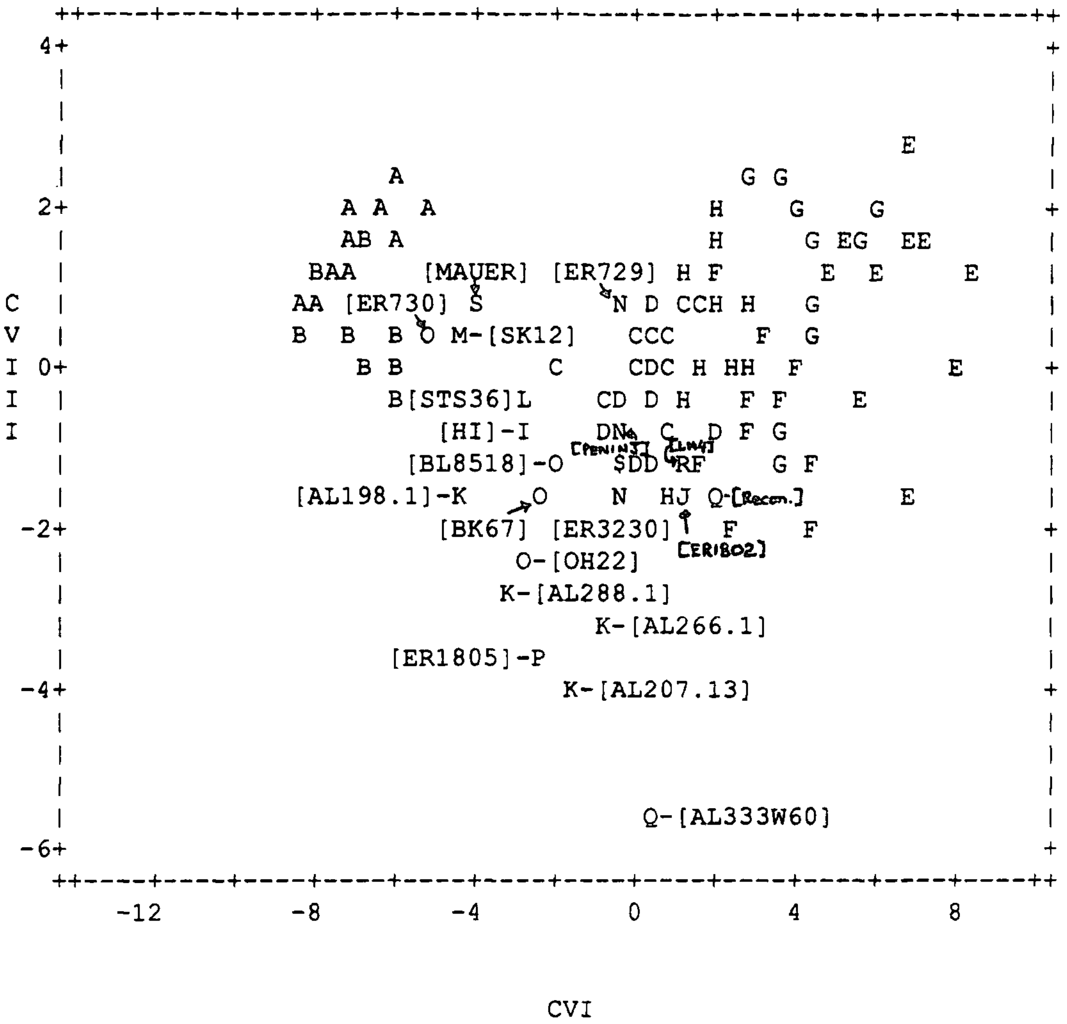
Axis III does not separate the groups very well with the scores of most groups dispersed along this axis. Fossils falling outside the range of pongids and *H. sapiens* are OH 22, KNM-ER 1805, A. L. 288.1, 266.1, 207.13, and 333w.60. SK 12 has a score close to those of *H. sapiens*. The *A. boisei* scores are close to those of *Pan* with a range less than that for male *Gorilla*. STS 36 has a score like HI, intermediate between *H. sapiens* and the pongids. Of the *A. afarensis* specimens, the range, including the reconstructed mandible and A. L. 198.1, is as great as that for *Gorilla*. The pattern of the scores does not follow that for *Gorilla* and *Pongo*, where males have higher and females lower values, which may indicate that the sample is heterogeneous. KNM-ER 1802 has a score close to that of LH 4 while that of KNM-ER 1805 is close to the scores for other *A. afarensis* specimens. Most African *H. erectus* specimens have close scores on this axis to one another and to HI. KNM-ER 730 and the Mauer mandible have scores close to those of *H. sapiens*.

The variables with the highest correlation with CVIII are M5- symphyseal height and M8- internal breadth. Overall, the results depict a decrease in size from the larger pongids to smaller pongids and larger hominids to smaller hominids.

When the sample is reclassified with respect to the original groupings, a number of "misclassifications" occur. The reclassification analysis lists both the highest probability group and the second highest probability group. Of the modern comparators, one *Pan* female is classified as a *Pongo* male (highest probability group - 1st choice) or LH 4 (second highest probability group - 2nd choice). Two *Pan* males are classified as *Pan* females (1st choice) or *Pan* females (2nd choice). One *Gorilla* male is classified as a *Pongo* male (1st choice) or a *Gorilla* male (2nd choice). Two *Gorilla* females are classified as *Pongo* females (1st choice) or *Gorilla* females (2nd choice). Three *Pongo* males are classified as *Gorilla* females or *Pongo* males. Finally, one *Pongo* female is classified as a *Gorilla* female or LH 4. Therefore each of the modern comparators has the highest probability of being assigned to its original group or, at least, of the pongids, being assigned to another pongid group.

Of the fossil hominids, KNM-ER 730 is classified as a male *H. sapiens* (1st choice) or with the Mauer mandible (2nd choice). BK 67 is classified as KNM-ER 1805 or *A.*

FIGURE 6.07B: MANDIBLE: PLOT OF CVIII WITH CVI



A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

afarensis. A. L. 266.1 is classified as *H. habilis* or *A. afarensis* and the reconstructed mandible as *H. habilis* or in its own group. The remaining fossils were 'correctly' assigned but it is interesting to note the 2nd choice group of these fossils. The 2nd choice group of LH 4 is *Pongo* female, that of KNM-ER 1802 LH 4, that of KNM-ER 1805 African *H. erectus*, that of A. L. 333w.60 *A. afarensis*, that of Mauer male *H. sapiens*, and that of HI African *H. erectus*.

6.4.2 Palate

Six characters are used to maximise the number of fossil hominids in this analysis (P1-4, P7, P9). The first three canonical variates account for 93.92 % of the total sample variance. CVI accounts for 65.16 %, CVII 22.14 %, CVIII 6.62 % of the total sample variance, and all three are highly significant ($p < .01$).

P3- alveolar length (.88) and P1- length (.77) have high loadings on CVI, P9- bicanine breadth (.4) has an intermediate one, the remaining characters have low loadings, and all are positive. The characters of length (P1, P3) would be expected to separate large from small palates, thus the larger pongids from *H. sapiens*, for example.

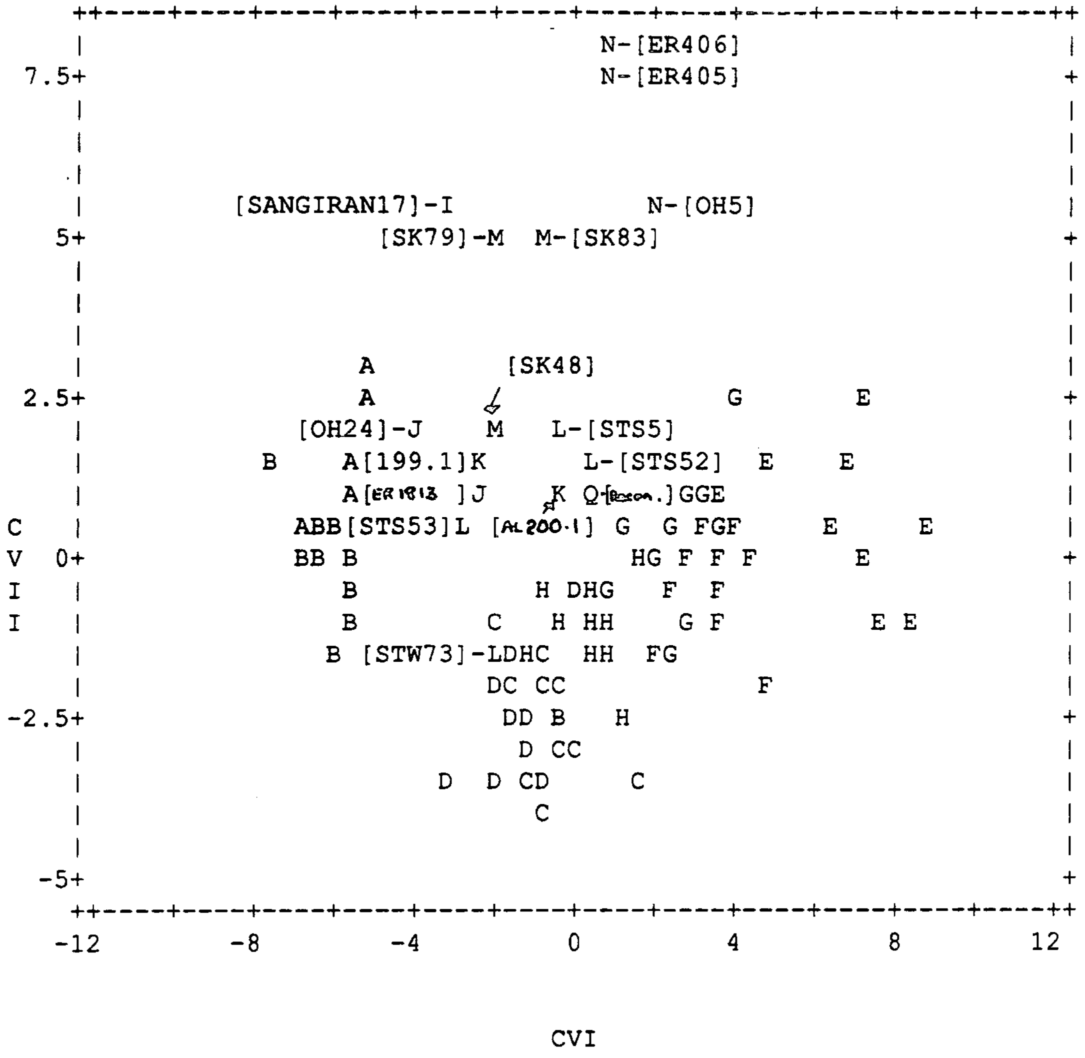
On CVII, only P4- external breadth (.6) has a high loading, P9- bicanine breadth (-.3) has an intermediate one, and the remaining characters have low loadings. This axis should separate hominids with wide versus narrow palates and probably the robust australopithecines, with their wide molars, from the other hominoids.

On CVIII, P2- internal alveolar breadth (.73) has the highest loading, and that of P9- bicanine breadth (.2) the lowest, the remainder being intermediate and all are positive. This CV should also distinguish between wide and narrow palates and possibly also males from females as well.

Figure 6.08A distinguishes *H. sapiens* on the left side of the plot, *Gorilla* males on the right side of the plot, and robust australopithecines and Sangiran 17 in the top part of the plot. Male and female *Pan*, some *Pongo* females, and STW 73 are located at the bottom part of the plot. The remaining hominids are located in the middle of the plot; some closer to *H. sapiens*, like OH 24; some closer to pongids like STS 52, the *A. afarensis* reconstruction, and A. L. 200.1; while STS 53, KNM-ER 1813, A. L. 199.1, SK 48, and STS 5 are intermediate.

Axis I is discriminating on the basis of size with *H. sapiens* having the smallest, and *Gorilla* male the largest, scores. On axis II, the robust australopithecines and Sangiran 17 have the largest, and *Pan* the smallest, scores. There is some overlapping

FIGURE 6.08A: PALATE: PLOT OF CVII WITH CVI



```
      ++----+----+----+----+----+----+----+----+----+----+----+---++
      |                               N-[ER406]                    |
   7.5+                               N-[ER405]                    +
      |                                                            |
      |                                                            |
      |                                                            |
      |         [SANGIRAN17]-I           N-[OH5]                   |
     5+                  [SK79]-M  M-[SK83]                        +
      |                                                            |
      |                                                            |
      |                                                            |
      |                 A       [SK48]                             |
   2.5+                 A                      G       E           +
      |             [OH24]-J    M  L-[STS5]                        |
      |           B   A[199.1]K      L-[STS52]   E    E            |
      |               A[ER1813 ]J   K Q-[Recon.]GGE                |
  C   |            ABB[STS53]L [AL200·1] G  G FGF    E    E        |
  V  0+            BB B                 HG F F F       E           +
  I   |                B           H DHG   F  F                    |
  I   |                B        C   H HH    G F        E E         |
      |               B [STW73]-LDHC  HH  FG                       |
      |                        DC CC            F                  |
  -2.5+                         DD B    H                          +
      |                           D CC                             |
      |                      D  D CD     C                         |
      |                            C                               |
      |                                                            |
    -5+                                                            +
      ++----+----+----+----+----+----+----+----+----+----+----+---++
     -12        -8        -4         0         4         8        12

                                   CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

of male and female scores but with males generally having larger scores than females (except with *Pan* where scores of both sexes overlap considerably).

Of the *A. robustus* specimens, SK 79 and 83 are males and SK 48 a female which accounts for their separation but the range of this species is smaller than that of the modern groups. STS 5 and 52 have larger scores than STS 53 and STW 73 but this group is not any more variable than *Gorilla* males. *A. boisei* has a smaller range of scores than any of the modern groups with OH 5 having a smaller score than KNM-ER 405 and 406. There is not much separation between the two *A. afarensis* specimens and the reconstructed cranium, but note that A. L. 199.1 has a larger score than the male *A. afarensis* specimens, opposite to the pongid pattern of sexual dimorphism. OH 24 and KNM-ER 1813 have close scores on axes I and II. Finally, Sangiran 17 has a high score close to that of SK 79.

Figure 6.08B shows *H. sapiens* in the upper left quadrant of the plot and *Gorilla* males in the upper right quadrant. On axis II the scores are widely dispersed and with many groups having overlapping values. Again there is some separation of the sexes within groups, especially in *Gorilla* and *Pongo*. Within *A. robustus* SK 83 and 79 are most widely separated but no more than the extreme *H. sapiens* males. The *A. boisei* specimens have close scores on this axis. STS 5, 53, and STW 73 have close scores while STS 52 has a score which is the lowest of all the hominids, probably due to its immature status. Of the *A. afarensis* specimens, the males have higher scores than A. L. 199.1. The *H. habilis* specimens have close scores on this axis while Sangiran 17 has a score intermediate between *H. sapiens* and *Pan*.

The groups seem to be separating mainly on the basis of size with some shape differences accounting for the within and between group variation. The length and width of the palate is determined by the size of the dentition which accounts for the separation of the robust australopithecines from the other groups in figure 6.08A. The overlapping scores of the other groups is due to within group size variation where small members of one group overlap in size with large members of another group.

When the groups are reclassified with respect to the initial groupings, a number of individuals are "misclassified". Amongst the modern comparators, one *H. sapiens* male is classified as *H. sapiens* female (1st choice) or *H. sapiens* male (2nd choice). One *H. sapiens* male is classified as *H. habilis* (1st choice) or *H. sapiens* male (2nd choice). One *Pan* female is classified as *Pongo* female or *Pan* female and two *Pan* males as *Pan* females or *Pan* males. Two *Gorilla* females are classified as *Pongo* males or *Gorilla* females and one *Gorilla* male as *Gorilla* female or *Pongo* male. One *Pongo*

FIGURE 6.08B: PALATE: PLOT OF CVIII WITH CVI

```
     ++----+----+----+----+----+----+----+----+----+----+----+----++
    4+                                                             +
     |                                                             |
     |                A                                            |
     |              B  A               G                           |
     |               B                      G       E              |
    2+                        [SANGIRAN17]           EE            +
     |           B B  B                                            |
     |             AB A     I     C   H    G    E   EE   E         |
C    |                B    [SK83]-MC H  FGG FG            E        |
V    |               B         C   DD G      E F                   |
I   0+                B       DCCH   H[ER405]F F                   +
I    |                 [SK48]- MDDC   HN CG   F  F                 |
I    |                 A    D   DCC   H   G  G                     |
     |             [OH24]-J  L  D  FC  HH  FF                      |
     |             [STS53] [STW73]-L H  L-[STS5] NF                |
   -2+               [ER1813]-JD   H QN-[ER406] [OH5]              +
     |                  [SK79]-M  D  [Recon.]                      |
     |                             K-[AL200.1]                     |
     |                                                             |
     |                       K-[AL199.1]                           |
   -4+                                                             +
     |                                                             |
     |                               L-[STS52]                     |
     |                                                             |
     |                                                             |
   -6+                                                             +
     ++----+----+----+----+----+----+----+----+----+----+----+----++
    -12        -8        -4         0         4         8        12

                                   CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

male classifies as *Gorilla* female or *Pongo* female while another *Pongo* male classifies as *Pongo* female or *Pongo* male. One *Pongo* female classifies as *A. africanus* or *Pongo* female and another *Pongo* female as *Pan* female or *Pongo* female. The majority of the modern comparators, however, were accurately reclassified.

Of the fossil specimens, STW 73 classifies as *Pan* female (1st choice) or *A. africanus* (2nd choice) while STS 53 classifies as *H. habilis* or *A. africanus*. This could have occurred due to the greater prognathism of STS 5 making its palate longer and creating large within-group variability. The other fossils are correctly classified, that is are classified into the group to which they were originally assigned, but it is interesting to note the 2nd choice groups of these individuals. The 2nd choice group of the *A. boisei* specimens was *A. robustus*; that of KNM-ER 1813, *A. africanus*; OH 24, male *H. sapiens*; A. L. 199.1, *A. africanus*; A. L. 200.1, 333w.60/ reconstruction; SK 48 and 79, *H. habilis*; SK 83, *A. boisei*; STS 5, *A. robustus*; STS 52, *A. afarensis*; the reconstructed palate, *A. afarensis*; and Sangiran 17, *A. robustus*. Thus larger palates tend to be allocated to *A. robustus*, *A. boisei*, or to the group containing A. L. 333w.60/ reconstruction while the smaller palates are allocated to *H. habilis*, *A. africanus*, or *H. sapiens*.

6.4.3 Base

Eleven basicranial measurements are used in this analysis to obtain the maximum number of fossil hominids (B3-13). The first three CV's account for 88.15 % of the total variance. The fourth CV accounts for less than 5 per cent of the variance and none of the variables have high loadings thus this CV will not be discussed in this analysis. CVI accounts for 60.58 %, CVII 20.50 %, and CVIII 7.07 % of the total variance and all are highly significant ($p < .01$).

None of the characters has high loadings for CVI. The highest loadings are B5- bistyloid width (.34), B9- biinfratemporal fossa width (.31), B10- tympanic-carotid canal chord (-.32), and B11- carotid canal - petrous temporal (-.36). The remaining characters have low loadings.

All the characters are positive on CVII. B3- bitympanic width (.67), B4- bistylomastoid width (.65), B7- bipetrous width (.53), B10- tympanic - carotid canal (.5), B12- biinfratemporal line - bitympanic line (.5), and B13- biforamen ovale line - bitympanic line have high loadings. B5- bistyloid width (.34), B6- bicarotid canal (.38), B8- biforamen ovale (.41), B9- biinfratemporal fossa width (.43), and B11- carotid canal - petrous chord (.41) all have intermediate loadings. Groups should be separated by size on the basis of width measurements while B7 might separate those individuals with sagittally from those with coronally oriented petrous bones.

On CVIII, B7-bipetrous width (.62) and B13-biforamen ovale line-bitympanic line (-.5) have high loadings while the remaining characters have low ones. This axis may separate individuals with flexed from those with unflexed bases but one would not expect a great separation of groups due to the common functional role of the base relating, for example, to balance.

Figure 6.09A shows Sangiran 17 in the upper right quadrant, male *Gorilla* in the upper left quadrant and *Pan* in the lower left quadrant. On axis I *H. sapiens* has the highest and the pongids the lowest scores with most of the hominids having intermediate scores. TM 1517 has a score close to those of *Gorilla* females while the *A. boisei* specimens are located in the centre of the plot. STS 5 and 19 have close scores while MLD 37/38 has a score closer to those of the *Pan* specimens but the range of scores of *A. africanus* is less than that of *H. sapiens.* The *A. afarensis* reconstructed cranium has a score which is close to the *H. sapiens* scores. The *H. habilis* specimens have close scores on axis I while KNM-ER 1805 has one close to *Gorilla* females and *Pongo* males. The African *H. erectus* specimens have close scores on this axis and the range, even if Sangiran 17 is included, is smaller than that of *Gorilla* but the separation of these two groups may be an indication of regional or temporal differences. Thus axis I is separating groups on the basis of the size of the base with pongids having the narrowest, *H. sapiens* and Sangiran 17 the widest, and the majority of fossil hominids having intermediate, sized bases.

On axis II, many of the scores of the modern hominoids overlap, but with *Pan* having the lowest scores, *H. sapiens*, *Pongo*, and *Gorilla* females with intermediate scores, and *Gorilla* males with the highest scores. *A. africanus* and *H. habilis* have low scores on this axis due to their narrower bases and relatively smaller crania compared to the other hominids. The robust australopithecines and the *A. afarensis* reconstruction have wider bases related to their wider, more robust mandibles which necessitate a wider cranial base. The African *H. erectus* specimens fall within the *H. sapiens* range on this axis but they possess relatively wider bases compared to *H. sapiens.* So, although the cranial capacity of these specimens is smaller relative to *H. sapiens*, their wide bases result in their scores being comparable to *H. sapiens.* KNM-ER 1805 has a high score on this axis, not so much due to the width of its base, but to its measurements for B12 and B13 which, in the PCA, showed this specimen to possess a peculiar basicranial configuration. The high position of Sangiran 17 on this axis is not only due to its possessing a larger cranial capacity than the African *H. erectus* specimens but also a wider base relative to *H. sapiens.*

```
    FIGURE 6.09A: BASE: PLOT OF CVII WITH CVI
    ++----+----+----+----+----+----+----+----+----+----+----+----++
 7.5+               E                                             +
    |                                                             |
    |            E   E                          I-[SANGIRAN17]    |
    |                                                             |
    |            E                                                |
   5+             EE                                              +
    |              E  E                                           |
    |             E                                               |
    |              E        [ER1805]                              |
    |              G                                              |
 2.5+               G     P[ER3733]-O     O-[OH9] AA              +
    |             F G                                             |
    |                  FFGF                     A  A              |
    |             F  FGGF             O-[ER3883]  AA A            |
C   |             G    FF [ER406]  N-[OH5]      A B   B           |
V  0+              H   GH       N    N     A B      B             +
I   |               G F H      [ER407]    Q  B BB                 |
I   |             H   C      M-[TM1517][Recon.]B                  |
    |                 G HC  H       J-[ER1813] B  B               |
    |                 C    H [STS5]                               |
-2.5+                 CDCH H     L J-[OH24]                       +
    |                CDDHD C                                      |
    |                 CC   L-[MLD37/8]                            |
    |                  CD DD      LJ-[SK847]                      |
    |                  DD    [STS19]                              |
  -5+                  D                                          +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
         -8        -4         0         4         8        12

                                   CVI

 A:MALE H.SAPIENS B:FEMALE H.SAPIENS  C:MALE PAN D:FEMALE PAN
 E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
 I:ASIAN H.ERECTUS     O:AFRICAN H.ERECTUS          S:MAUER
 J:H.HABILIS           P:ER1805
 K:A.AFARENSIS         Q:AL333W60/ RECONSTRUCTION   R:LH4
 L:A.AFRICANUS         M:A.ROBUSTUS                 N:A.BOISEI
 $:Multiple occurrence
```

These findings agree with studies by Dean and Wood (1981, 1982) who found similarities of the base between *A. boisei* and members of the *Homo* lineage. A large, wide, mandible requires a wider base than a smaller, narrower, mandible. Large mandibular condyles would have a more profound effect on the modelling of the mandibular fossa, possibly great enough to effect the angle of the petrous temporal (but see Dean 1988 for a discussion of how the petrous temporal bone is affected during growth in pongids and humans). Cranial volume would also have an effect on the width of the base; a larger brain requiring a wider platform to rest on which in turn would effect the size, and perhaps the thickness, of the vault bones (Demes 1985). Thus I believe that the morphological similarity between *A. boisei* and *H. erectus* is not due to any direct phyletic relationship, but rather to similar solutions to different functional problems.

Figure 6.09B reveals the pongids concentrated in the left half of the plot, *H. sapiens* more widely dispersed in the right half of the plot, and most fossil hominids intermediate between the two. On axis III, the pongids and *H. sapiens* have overlapping scores and the *A. africanus* and African *H. erectus* specimens fall within this range of scores. Of the *H. habilis* specimens, KNM-ER 1813 and OH 24 fall within the hominoid range but SK 847 has a low score due to its low, estimated, value for B7. KNM-ER 1805 has the lowest score on this axis. The low value of B7 for this specimen is estimated but it has a large value for B13. OH 5 and KNM-ER 407 fall within the hominoid range but KNM-ER 406 has a lower score due to its low, estimated, value for B7. This is also the reason for the low position of TM 1517. The high position of the reconstructed *A. afarensis* skull is due to a large, estimated, value for B7 (A. L. 333.45 has a lower estimated value for B7). Finally, Sangiran 17 has a high value for B7, outside the range of values for even *H. sapiens*. This means the specimen was incorrectly measured, the information was incorrectly transcribed, or else this specimen has widely separated petrous bones compared to *H. sapiens* as well as other hominoids.

When individual specimens are reclassified with respect to the original groups a number of "misclassifications" occur. Amongst the modern comparators, two female *H. sapiens* classify as male *H. sapiens* (1st choice) or female *H. sapiens* (2nd choice). One *H. sapiens* male classifies as female (1st choice) or male (2nd choice) *H. sapiens*. Three male *Pan* classify as female or male *Pan* and one female *Pan* as male or female *Pan*. One *Gorilla* female classifies as a *Pongo* male (1st choice) or *Gorilla* female (2nd choice). Two *Pongo* males classify as female or male *Pongo* while two *Pongo* females the opposite classification occurred. One *Pongo* female classifies as a *Pan* male or a

FIGURE 6.09B: BASE: PLOT OF CVIII WITH CVI

```
    ++----+----+----+----+----+----+----+----+----+----+----+----++
 7.5+                                                             +
    |                                           I-[SANGIRAN17]    |
    |                                                             |
    |                                                             |
    |                                                             |
   5+                                                             +
    |                                                             |
    |                                                             |
    |                                     Q-[Recon.]              |
    |                      H                                      |
 2.5+                   H                       B                 +
    |             H        CH                      A              |
    |             $HG G$$                                         |
C   |               G $GHHF                    BA  A              |
V   |              E  $ DGD   [MLD37/8]   A     A AAB             |
I  0+            E $E FFD  $/ [STS19] [ER3883] B  B  A            +
I   |             EE C $F$ L     LL   O      B B  B  A            |
I   |            EF  EED    [STS5]  O-[ER3733]B   A               |
    |                FCFF           J-[ER1813]                    |
    |             E          [OH5]-N      O-[OH9]                 |
-2.5+                       [OH24]-J N-[ER407]                    +
    |                                                B            |
    |                                                             |
    |                              J-[SK847]                      |
    |                                                             |
  -5+               [TM1517]-M                                    +
    |                          N-[ER406]                          |
    |                     P-[ER1805]                              |
    |                                                             |
    |                                                             |
-7.5+                                                             +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
         -8        -4         0         4         8         12


                                   CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

Pongo female.

None of the fossil specimens is misclassified. The second choice group of the fossils is as follows: KNM-ER 406 and 407, *H. habilis*; OH 5, African *H. erectus*; KNM-ER 1805, *A. robustus*; KNM-ER 1813, *A. boisei*; OH 24 and SK 847, *A. africanus*; African *H. erectus*, *A. boisei*; MLD 37/8, *Pan* female; STS 5 and 19, *H. habilis*; TM 1517, *H. habilis*; reconstruction, African *H. erectus*; and Sangiran 17, male *H. sapiens*. This follows the position of specimens on axis I with MLD 37/8, TM 1517, and KNM-ER 1805 having small, *A. africanus*, *H. habilis*, *A. boisei*, and African *H. erectus* intermediate, and the reconstruction and Sangiran 17 large, scores on this axis.

6.4.4 Vault

Eight characters are used in this analysis (V1, V3-6, V10-12) because this allows a larger number of fossil hominids to be compared than if all vault measurements are used. The first three CV's account for 96.34 % of the total sample variance. CVI accounts for 84.42 %, CVII 9.59 %, and CVIII 2.34 % of the variance and all are highly significant ($p < .01$).

All the loadings are positive for CVI. A number of characters have large loadings: V1- frontal breadth (.54), V3- frontal chord (.5), V4- frontal chord (.5), and V10- supraglabellare - bregma chord (.56). The remaining characters have intermediate loadings. V3- frontal chord (.4) has the highest loading for CVII, V1- frontal breadth (-.32) and V12- inion arc (.3) have intermediate ones, and the remaining characters have low loadings. Not all the characters have positive loadings for CVII. V1- frontal breadth (-.73) has a high loading for CVIII. V11- inion chord (.4) and V12- inion arc (.31) have intermediate loadings, the remaining characters have low loadings, and most loadings are negative.

Figure 6.10A shows some overlapping of groups. *H. sapiens* is located in the lower right quadrant and most pongids in the left half of the plot. *Gorilla* males are distinguished from the other pongids, being located in the upper half of the plot. The fossil hominids are located in the centre and in the right half of the plot. On axis I, some Asian *H. erectus* scores overlap with scores for *H. sapiens* and scores for African *H. erectus* fall within the Asian *H. erectus* range. KNM-ER 1470 has a score close to that of Pithecanthropus I and KNM-ER 3733. KNM-ER 406, OH5, KNM-ER 1813, OH16, STS 5, and STS 17 have scores which fall within the male *Gorilla* range on axis I.

On axis II the scores of most of the hominoids overlap. KNM-ER 3883 and

FIGURE 6.10A: VAULT: PLOT OF CVII WITH CVI

```
    ++----+----+----+----+----+----+----+----+----+----+----+----++
   8+                                                             +
    |                        E                                    |
    |                        E                                    |
    |                             E                               |
    |                         E                                   |
   6+                                                             +
    |                           E                                 |
    |                           E                                 |
    |                   E                                         |
    |                                                             |
   4+                       EE                                    +
    |                                       O-[OH9]               |
    |                                       O-[ER3883]            |
    |                                                             |
    |                                                             |
   2+                                      I-[SKULL3]             +
    |                [ER406]-N  E [ER1470]                        |
    |           C   $  [OH16]-JJ      J O-[ER3733]                |
C   |             C   F[ER1813]       I     I-[SKULLII]           |
V   |            DCF F F   L    N-[OH5][PITHI]    I-[SANGIRAN17]  |
I  0+           D$$$ F  [STS71]    [SKULLIII]-I  I-[SKULLI]       +
I   |          C  D$CF                                 B  BA      |
    |          HGD               L-[STS5]          A  $           |
    |         D CD                             B   B              |
    |     H  HHGGG                                  B  BAA        |
  -2+         H HG F                                 ABA    A     +
    |        HG  G                                   BB  A     A  |
    |         GH                                                  |
    |                F                                            |
    |                                                             |
  -4+                                                             +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
         -8        -4         0         4         8        12

                             CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

OH 9 have larger scores than the other *H. erectus* specimens, close to male *Gorilla* scores which are also higher than the other hominoids. KNM-ER 3733 has a much lower score, falling within the *H. sapiens* range. Thus African *H. erectus* seem to be following the *Gorilla* pattern of sexual dimorphism.

The Asian *H. erectus* specimens have scores that are larger than those of *H. sapiens* and smaller than OH 9 and KNM-ER 3883 but the range of Asian *H. erectus* is small, comparable to that of *H. sapiens.* These specimens do not seem to be following the *Gorilla* pattern of sexual dimorphism. Skull 3 and Pithecanthropus I are likely females (due to their smaller cranial capacities and scores on axis I) but they have higher scores on axis II than the other Asian *H. erectus*, including the male, Sangiran 17. Instead, these specimens seem to have a pattern of sexual dimorphism like that of *H. sapiens* with overlapping values of males and females. These patterns of sexual dimorphism within *H. erectus* emphasise the differences between the African and Asian samples.

The *H. habilis* specimens have a small range of scores as do the *A. boisei* crania while the range of *A. africanus* is comparable to that of either sex of *H. sapiens.*

Axis I seems to be discriminating on the basis of overall size while axis II involves both size and shape. Frontal arc (V3) will distinguish domed from flatter vaults but this measurement is influenced by the size of glabella projection. Thus an individual with a large frontal and small glabella projection could have a similar score to ones with a small frontal and large glabella projection. This accounts for the overlapping of positions on axis II of pongids, most of the fossils, and *H. sapiens. Gorilla* males have the largest glabella area of all the hominoids which accounts for their high scores on axis II while OH 9 and KNM-ER 3883 have robust supraorbital tori but also larger frontals than *Gorilla* males.

In figure 6.10B, there is a slightly larger spread of groups. *H. sapiens* is again in the right half of the plot and is spread within the upper and lower right quadrants. On axis III, most of the fossil specimens fall within the range of *H. sapiens* and the pongids. The *A. africanus* specimens, KNM-ER 1470 and 1813, and KNM-ER 3883 fall outside the *H. sapiens* range, though all but STS 71 fall within the pongid range of scores. The large score of this latter specimen is due to a low, estimated, value for V1 and high values for V11 and V12 relative to the other hominids. The Asian *H. erectus* specimens have a small range of scores on this axis. That of African *H. erectus* is larger, but smaller than the range of *H. sapiens.* OH 9 and KNM-ER 3733 have low scores, the lowest of all the hominids (but within the *H. sapiens* range)

FIGURE 6.10B: VAULT: PLOT OF CVIII WITH CVI

```
    ++----+----+----+----+----+----+----+----+----+----+----+----++
   6+                                                             +
    |                                                             |
    |                      L-[STS71]                              |
    |                                                             |
    |                                                             |
   4+                                                             +
    |                                                             |
    |          H      [ER1813]-J L-[STS5]                         |
    |                                                             |
    |                                 J-[ER1470]                  |
   2+           G                        [ER3883]                 +
    |        HH  G   F       E              O      [SKULLI]       |
    |          GH      F        E  [SKULLIII]-I  I    B           |
 C  |        HG      [ER406]-NJ-[OH16]I-[PITHI]B     B            |
 V  |         HH GF          E  N E        II         BA A A      |
 I 0+         G  DCF FF   [OH5] $[SKULL3] [SKULLII]BB   A   A     +
 I  |     H   $ H  $GF      EE                        BB  B       |
 I  |           G  D    E                                A        |
    |          CDD C                  [OH9]-O     IA              |
    |           C$C F          [ER3733]-O             AB          |
  -2+             $ C                   [SANGIRAN17] A            +
    |            D                                             A  |
    |                                                             |
    |                         E                                   |
    |                                                             |
  -4+                                                             +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
         -8        -4         0         4         8        12

                             CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

while KNM-ER 3883 has a larger score with similar measurement values to Skull III for a number of variables. The *H. habilis* specimens have a larger range on this axis than on axis II with OH 16 falling within the *Gorilla* male and *A. boisei* range and KNM-ER 1470 and 1813 having larger scores. The values of V11 and 12 are estimates for OH 16, a greatly fragmented specimen that has been reconstructed, and which may be underestimated. Axis III is demonstrating some separation on the basis of size (V1) but mostly on the basis of shape.

Axis I reflects the increase of hominid cranial dimensions during the Pleistocene. It also shows a separation of the australopithecines from *H. erectus* due to the difference in cranial proportions of the two groups. For example, the frontal region of *A. boisei* is much lower, with a more marked post-orbital constriction than the later hominids. Also, the parietals are longer, and the occipital is longer, lower, and flatter, than in the later hominids. The low vault of of *A. boisei* is due to a shallower, broader, biparietal arch and the fact that the neurocranium is hafted to the face at a lower position than in *A. africanus* and thus the differentiation of these two species in figure 6.10B reflects the differences in the proportions and structure of the vault.

The differences between *A. africanus* and *H. habilis* on the one hand, and *H. erectus* on the other, are due to the greater size, widening of the frontal and occipital regions, and an increase in height of the skull of the latter group, and thus a combination of size and shape factors.

When individuals are reclassified with respect to the original groups a number of misclassifications occur. Amongst the modern comparators, three female *H. sapiens* classify as male (1st choice) or female (2nd choice) *H. sapiens.* Two male *H. sapiens* classify as female or male *H. sapiens.* One *Pan* male classifies as *Gorilla* female or *Pongo* male; three *Pan* males classify as female or male *Pan*; and two *Pan* females classify as *Pan* males or females. Two *Gorilla* females classify as *Pongo* males or *Pongo* females; one *Gorilla* female classifies as *Pan* male or female; and one *Gorilla* male classifies as *A. boisei* or *H. habilis.* Three *Pongo* males classify as *Pongo* females or males; one *Pongo* male as *Gorilla* female or *Pan* male; and one *Pongo* female as *Pongo* male or female.

None of the fossils is misclassified with respect to the original groups. It is interesting to note, however, that the second highest probability of group assignment for KNM-ER 1470 is African *H. erectus*; for KNM-ER 1813, *A. africanus*; and OH 16, *A. boisei* (due to the low measurements for V11 and 12). KNM-ER 3733 has *H. habilis* as its second highest probability group; KNM-ER 3883 and OH9, Asian *H.*

erectus; Sangiran 17 and Skull I, female *H. sapiens*; Pithecanthropus I, *H. habilis*; the remaining Asian *H. erectus*, African *H. erectus*; both *A. africanus* specimens, *H. habilis*; and OH5 and KNM-ER 406, *H. habilis* (probably due to the values of OH 16 for V11 and V12).

6.4.5 Face

Twelve characters are used in this analysis of the facial region (F1-4, F8-13, F21, F23). The first three CV's account for 87 % of the variance. The first CV accounts for 40.39 %, CVII 37.03 %, and CVIII 9.49 % of the total sample variance and all are highly significant ($p < .01$).

On CVI all the loadings are positive. F10- zygomaxillary subtense (.5), F11- subspinale- zygomaxillary chord (.58), F12- upper facial height (.54), and F13- nasal height (.7) have high loadings on this CV. F1- biorbital breadth (.4), F4- orbit height (.41), F8- upper facial breadth (.41), F9- bimaxillary chord (.41), F21- cheek height (.44), and F23- lateral facial length (.43) have intermediate values while F3- orbit breadth has the only low loading on this CV. This CV should discriminate on the basis of overall size while also causing some separation between groups possessing greater or lesser facial prognathism or projection.

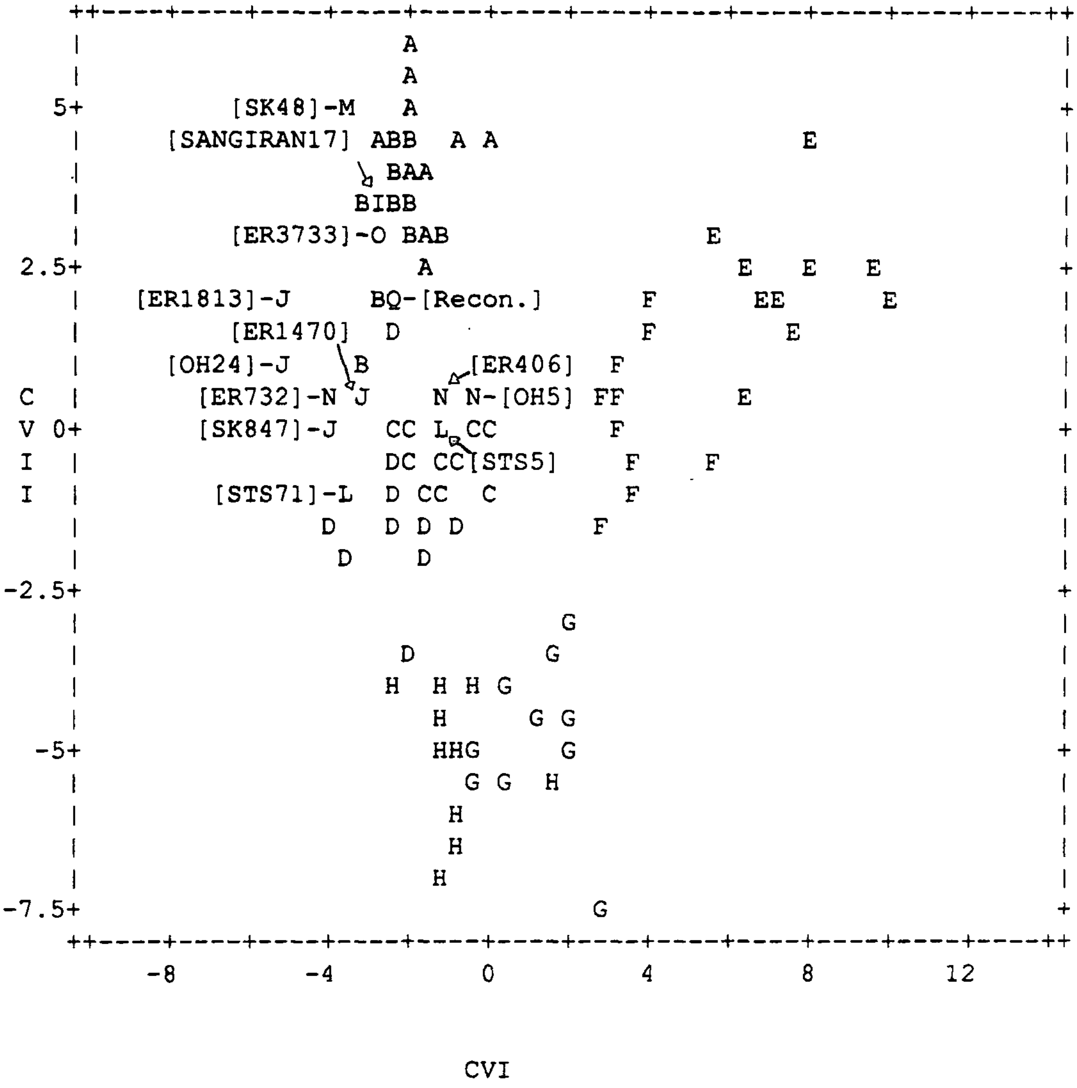
On CVII, F1- biorbital breadth (.6) has the highest value, F2- interorbital breadth (.35), F3- orbit breadth (.31), and F8- upper facial breadth (.4) have intermediate values. The remaining characters have low values and not all are positive. This CV should discriminate on the size and shape of the orbits and orbital area.

For CVIII, F9- bimaxillary chord (.57) and F21- cheek height (.53) have the highest values. F1- biorbital breadth (.35), F3- orbit breadth (.32), F11- subspinale - zygomaxillare chord (.35) and F23- lateral facial length (.3) have intermediate values. The remaining characters have low loadings and not all are positive. This CV should distinguish groups on the basis of cheek area robusticity and possibly facial prognathism or projection.

Figure 6.11A shows *Gorilla* in the upper right part of the plot and *Pongo* in the lower half of the plot. *Pan* and *H. sapiens* are in the left half of the plot with *H. sapiens* having higher scores than *Pan*. The fossils are located amongst the *H. sapiens* and *Pan* scores. This plot shows some discrimination by sex amongst *Gorilla*, *Pongo*, and *Pan* but not as much within *H. sapiens*.

On axis I, *Gorilla* crania have the largest scores with those of *Gorilla* males larger than those of the females. *Pongo* males have the next highest scores with

FIGURE 6.11A: FACE: PLOT OF CVII WITH CVI



A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

Pongo females, *Pan*, and *H. sapiens* having overlapping scores.

KNM-ER 1813, OH 24, KNM-ER 732, SK 847, STS 71, and SK 48 all have scores outside the range of *H. sapiens.* All of these have scores within the *Pan* range except KNM-ER 1813 and OH 24 which have the lowest scores of all the hominoids, possibly due to the fact that they are both females. The remaining fossil hominids have scores that fall within the *Pan*, *H. sapiens*, and female *Pongo* range. This axis is discriminating on the basis of size and robusticity of the face. STS 5 has a score close to that of KNM-ER 406 and OH 5, not because it is more robust than STS 71, but because its face projects more giving a measurement that compares to those of the *A. boisei* specimens.

Axis II shows *Pongo* to be isolated from the other hominoids due to this pongid's distinct shape of orbital area. *Pan* and female *Gorilla* have the next largest scores. Within this range are located *A. africanus* and *A. boisei* which have close within-group scores. The scores of *H. habilis* overlap the range of *Pan* and *H. sapiens* scores with KNM-ER 1470 and SK 847 closer to *Pan* and KNM-ER 1813 and OH 24 closer to *H. sapiens.* SK 847's position is likely affected by estimated values. The position of OH 24 and KNM-ER 1813 relative to KNM-ER 1470 is likely due to sex differences. Sangiran 17 and KNM-ER 3733 have close scores located within the *H. sapiens* sample, an indication of their close affinity to this latter group than to the australopithecines. The large score for SK 48 separates it from KNM-ER 732 on axis II, distinguishing between the females of the species of *A. robustus* and *A. boisei.* Finally, the reconstructed *A. afarensis* cranium is located between *H. sapiens* and *Pan.*

Axis II seems to be discriminating between the size and shape of the orbital area between groups. Note, however, that there is some indication of sexual dimorphism within *H. sapiens* and *Gorilla* on this axis but not within *Pongo* or *Pan.* Thus orbit size and shape can be sexually dimorphic trait in some species but within *A. boisei*, likely a highly dimorphic species, KNM-ER 732, 406, and OH 5 have close scores on Axis II. Thus this species does not follow the *Gorilla* pattern of sexual dimorphism, for this area of the cranium.

An examination of the original measurements for F1, F2, F3, and F8 (those with the highest loadings on axis II) provides some explanation of this phenomenon. For these characters *Gorilla* is dimorphic with male and females values overlapping slightly for F2 and F3, but not at all for F1 and F8. Within the *A. boisei* sample, KNM-ER 406 and OH 5 have closer values than either does to the smaller values of

KNM-ER 732. So there is some indication of sexual dimorphism within *A. boisei* for these characters (if KNM-ER 406 and OH 5 are males and KNM-ER 732 a female). However, the difference between the largest and smallest values of *Gorilla* for each of these characters is much greater than that between the values of KNM-ER 732 and the largest male *A. boisei* value (either OH 5 or KNM-ER 406 depending on which character is being examined). Thus the degree of sexual dimorphism is much less in *A. boisei* for these characters than in *Gorilla*, resulting in *A. boisei* having closer CV scores on axis II than the sexes of *Gorilla*.

Axis III (see figure 6.11B) shows a great overlap in the scores of the modern comparators with most fossil hominids isolated in the upper left quadrant. Fossils with the highest scores on this axis (eg. Sangiran 17, KNM-ER 406, 1470, OH 5, and SK 847) have measurement values similar to those of *H. sapiens* and *Pan* on axis I but measurement values similar to *Gorilla* and *Pongo* on axis III (ie. wider, more robust faces compared to other fossil hominids). Fossils with lower values like KNM-ER 1813, 732, STS 71, and STS 5 have scores close to those of *H. sapiens*, *Pan*, and female *Pongo*, that is smaller, more gracile, features. OH 5 is positioned closer to male *Gorilla* and *Pongo* because of its longer face (F12), nasal height (F13), and zygomaxillary subtense (F10) than the other *A. boisei* specimens, due to the incorrect positioning of the face (Williams 1984). It should have a higher score on this axis, closer to that of KNM-ER 406. The *A. boisei* range does not exceed that of *Gorilla* or *Pongo*. Many of STS5's measurements have values within the *Pan* range of measurement values which accounts for its low score on axis III. The reconstructed *A. afarensis* cranium has measurement values within the range of *H. sapiens*, *Pan* and *Pongo* for a number of characters. But for F2 (interorbital breadth) it has the highest value of all the hominoids which accounts for its low position on axis III. Thus axis III discriminates on the basis of shape characteristics of the orbital area, robusticity of the cheek area, and facial projection.

When the individuals are reclassified with respect to the original groupings a number of misclassification occur. Within the modern groups, two female *H. sapiens* classify as males (1st choice) or females (2nd choice) while one male *H. sapiens* classifies as a female (1st choice) or male (2nd choice). Three female *Pan* classify as males (1st choice) or females (2nd choice) while two male *Pan* classify as females or males. Two male *Pongo* classify as females or males.

Of the fossil hominids, only one is misclassified. KNM-ER 1470 classifies as African *H. erectus* (1st choice) or *H. habilis* (2nd choice). Of the remaining hominids, none is misclassified but it is interesting to note the second group choice. The second

FIGURE 6.11B: FACE: PLOT OF CVIII WITH CVI

```
    ++----+----+----+----+----+----+----+----+----+----+----+----++
  6+                                                              +
   |                  [SANGIRAN17]                                |
   |                   ↙                                          |
   |                 I   N-[ER406]                                |
   |    [OH24]-J    J-[ER1470]                                    |
  4+               M-[SK48]                                       +
   |              J-[SK847]       G                               |
   |                 O-[ER3733]                                   |
   |                           G                                  |
   |      [ER732]-N              G          E                     |
  2+  [ER1813]-J     [OH5]-N G                                    +
   |                     H                      E                 |
   |                     GH      G F      E  E       E            |
C  |                  HBAH G    G    FF                           |
V  |       [STS71]-L  BAA  G     G  F                             |
I 0+                B  B  A                                       +
I  |                  $$A  H G     F         E     E              |
I  |                  $BCHH      FF F       E                     |
   |                 AB$DHHCA   H          E   E                  |
   |               DBBDCDLD               F                       |
 -2+                  D [STS5] C                                  +
   |              D   D  CC         F                             |
   |                   C                                          |
   |         [Recon.]-Q  C  C                                     |
   |                                                              |
 -4+                                                              +
    ++----+----+----+----+----+----+----+----+----+----+----+----++
           -8        -4         0         4         8        12

                                  CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

group choice of KNM-ER 406, 3733, and SK 48 is *H. habilis*; that of OH 24 and SK 847, *A. boisei*; that of *A. africanus*, *Pan*; KNM-ER 732, *A. africanus*; KNM-ER 1813, female *H. sapiens*; OH 5, male *Pan*; *A. afarensis*, female *H. sapiens*; and Sangiran 17, African *H. erectus*.

6.4.6 Regional Combination

Seven variables are used in this regional combination analysis (B6, B8, B9, V1 V2, F1, F4) for the same reasons as given in the PCA. The first three CV's account for 93.19 % of the total sample variance. CVI accounts for 65.78 %, CVII 19.72 %, and CVIII 7.69 % of the variance and all three are highly significant ($p < .01$).

For CVI, V1- frontal breadth (.83) and V2- biparietal breadth (.68) have high loadings, B9- biinfratemporal fossa width (.34) has an intermediate loading, the remaining variables have low loadings, and most have positive values. This CV should discriminate groups on the basis of size of the vault and degree of post-orbital constriction.

F1- biorbital breadth (.91) has the highest loading on CVII while B8- biforamen ovale width (.35), B9- biinfratemporal fossa width (.3), and F4- orbit height (.31) have intermediate values. The remaining variables have low loadings and all are positive. This CV should separate groups on the basis of orbit size and shape and size of the anterior base.

For CVIII, B6- bicarotid canal width (.57), B9- biinfratemporal fossa width (.63) and F4- orbit height (.52) have high loadings while V2- biparietal breadth (.34) and B8- biforamen ovale width (.3) have intermediate ones. The remaining loadings are low and not all are positive. This CV should discriminate mainly wide from narrow skulls or on the basis of overall cranial size.

In figure 6.12A, *H. sapiens* is located in the right half of the plot, the pongids and australopithecines in the left half of the plot, and some fossil members of the genus *Homo* intermediate. *Gorilla* is located in the upper left quadrant while *Pan* and *Pongo* are in the lower left quadrant. There is some evidence of sexual dimorphism in *Gorilla* and *Pongo*, but not in *H. sapiens* and *Pan*.

Axis I seems to be discriminating on the basis of cranial size, with *H. sapiens* and Sangiran 17 having the highest scores, African *H. erectus* and *H. habilis* intermediate scores, and the australopithecines and pongids having the lowest scores. Of the *H. erectus* specimens there is some separation between African and Asian individuals, greater than that found in *Pan*, less than that found in *H. sapiens*, but about the

FIGURE 6.12A: REGIONAL COMBINATION: PLOT OF CVII WITH CVI

```
     ++----+----+----+----+----+----+----+----+----+----+----+----++
  7.5+                 E                                           +
     |                  E                                          |
     |                                                             |
     |                    E                                        |
     |                  E                                          |
    5+                   E  E                                      +
     |              E    E    E                                    |
     |                                                             |
     |                  F  E                                       |
     |                               O-[ER3883]                    |
  2.5+               F  F                O-[ER3733]                +
     |                  F F                                        |
     |        [ER406]-NFF F                    I-[SANGIRAN17]      |
     |                 F  CC N-[OH5]             A  A              |
C    |             [ER732] F  D   J-[ER1470]       AA A            |
V   0+              G  GDCNC   C                B BBB              +
I    |                 GD  CDJ-[OH24]          B  B A        A     |
I    |                  CGCGD                 B A  A A             |
     |                GD C C   J-[ER1813]    B       B             |
     |              G[Bacon.]-Q D                                  |
 -2.5+               G H  DDL-[STS5]                               +
     |              GHHG                       B                   |
     |           H  HH   HD                                        |
     |                                                             |
     |              H                                              |
   -5+               H H                                           +
     ++----+----+----+----+----+----+----+----+----+----+----+----++
          -8        -4         0         4         8        12

                              CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

same as that found in male *Gorilla* and *Pongo* (both sexes combined). The ranges of both *H. habilis* and *A. boisei* are about equal to that of *Pan*. STS 5 and the *A. afarensis* reconstruction both have scores within the *Pan* range indicative of their relatively small cranial size like that of the other australopithecines. Thus axis I is separating groups on the basis of vault size, showing a progression within the fossil sample from the australopithecines, to early *Homo*, to later *Homo* and *H. sapiens*.

On axis II, *Pongo* crania have the lowest scores, *H. sapiens*, *Pan*, and female *Gorilla* crania intermediate ones, and male *Gorilla* crania the highest, scores. Of the hominids, *A. afarensis*, *A. africanus*, and KNM-ER 1813 have the lowest, KNM-ER 732, 1470, 406, OH 5 and Sangiran 17 have intermediate, while KNM-ER 3733 and 3883 have the highest, scores. These latter fossils have similar values to *Gorilla* for F1, B8, and B9 whereas STS 5, *A. afarensis*, and KNM-ER 1813 have measurement values similar to *Pan* and *Pongo* on axis I and *Pan*, *Pongo*, and *H. sapiens* on axis II. None of the ranges of the fossil groups exceed those of the modern groups. Thus axis II is separating groups on the basis of biorbital breadth and the width of the anterior base.

In figure 6.12B, most scores overlap on axis III but with *Pan* having the lowest ones and most of the remaining individuals, intermediate scores. The *A. afarensis* reconstruction and Sangiran 17 both have high scores but B9 was estimated on both specimens. KNM-ER 3733 has a small measurement value for B9 like those of *H. sapiens* females while KNM-ER 3883 has a value for B9 like those of *H. sapiens* males. The range of African *H. erectus* scores is less than that of *Gorilla*. The range of African and Asian *H. erectus* scores combined is greater than that found in *Gorilla*. This may be due to the estimated value of B9 for Sangiran 17, otherwise it may be indicative of temporal and/ or regional differences between the two groups. KNM-ER 1813 and 1470 have the same scores for axis III. OH 24 has a lower score because it has lower measurement values for B6 and B9 but the *H. habilis* range is smaller than that of *Gorilla*. KNM-ER 406 and OH 5 have close scores on this axis with KNM-ER 732 having a lower score due to its smaller measurement values for most characters, but the range for *A. boisei* is smaller than that of *Gorilla*. STS 5 is closest to *Pan* in the size of most of its measurements which accounts for its low score on this axis. Thus axis II is separating groups on the basis of skull width. Individuals with wider bases either have larger cranial capacities than other hominoids, requiring a wider base platform, or else have large, wide mandibles which require a wide base. This accounts for the overlapping scores for species such as *H. sapiens* and *Gorilla*, for example as well those of *A. boisei*, *H. habilis*, and *H. erectus*.

FIGURE 6.12B: REGIONAL COMBINATION: PLOT OF CVIII WITH CVI

```
     ++----+----+----+----+----+----+----+----+----+----+----+----++
    6+                                                             +
     |                      [Recon.]                               |
     |                                                             |
     |                    Q                    I-[SANGIRAN17]      |
     |                                                             |
    4+                                                             +
     |                                                             |
     |                   G       [ER1813]                          |
     |              G G                                            |
     |                 G E     J  J-[ER1470]                       |
    2+              HHH   E                         BB             +
     |              GH GE                     B                    |
     |           H  HHGFF     E      O-[ER3883]    A               |
 C   |              G  H  F                                  A     |
 V   |      [ER406]  GN  E GEN-[OH5]           B  B                |
 I  0+              E  HF FE J-[OH24]           A BAA              +
 I   |               F EF                      B    A A            |
 I   |                 E$H D    [ER3773]-O   B     BA              |
     |                 FDC F                    BA   A             |
     |                 D  CCD                                      |
   -2+                   CDC                                       +
     |            [ER732]-NC  D                                    |
     |                    CCD                                      |
     |                 D  D L  C                                   |
     |                      D[STS5]                                |
   -4+                                                             +
     ++----+----+----+----+----+----+----+----+----+----+----+----++
          -8        -4         0         4         8        12

                              CVI
```

A:MALE H.SAPIENS B:FEMALE H.SAPIENS C:MALE PAN D:FEMALE PAN
E:MALE GORILLA F:FEMALE GORILLA G:MALE PONGO H:FEMALE PONGO
I:ASIAN H.ERECTUS O:AFRICAN H.ERECTUS S:MAUER
J:H.HABILIS P:ER1805
K:A.AFARENSIS Q:AL333W60/ RECONSTRUCTION R:LH4
L:A.AFRICANUS M:A.ROBUSTUS N:A.BOISEI
$:Multiple occurrence

When individual specimens are reclassified with respect to the original groupings a number of misclassifications occur. Two female *H. sapiens* classify as male (1st choice) or female (2nd choice) *H. sapiens* while three male *H. sapiens* classify as female (1st choice) or male (2nd choice) *H. sapiens*. Two female *Pan* classify as male (1st choice) or female (2nd choice) *Pan* and one male *Pan* classifies as female or male *Pan*. Finally two male *Pongo* classify as female or male *Pongo*.

Of the fossil specimens, KNM-ER 732 classifies as a *Pan* female (1st choice) or *A. boisei* (2nd choice). The second choice classification of the remaining fossils is as follows: KNM-ER 406 and OH 5, *A. africanus*; KNM-ER 1470, African *H. erectus*; KNM-ER 1813, *A. afarensis*; OH 24, *Pan* female; KNM-ER 3733, female *H. sapiens*; KNM-ER 3883, *H. habilis*; STS 5, female *Pan*; Sangiran 17, female *H. sapiens*; and *A. afarensis*, *H. habilis*.

6.4.7 Discussion

The CVA shows some interesting patterns within and between the modern and fossil species. In the analyses of the *H. erectus* base, vault, face, and regional combination, there is some indication of differences between groups. CVA will maximise the between group differences so this may be partially responsible for the results. In the mandible analysis, however, most African and Asian specimens group closely together with only KNM-ER 730 and the Mauer mandible separated. Also, in the vault analysis, there is an indication of different patterns of sexual dimorphism within the African and Asian samples. In the African sample, the placement of specimens follows the *Gorilla* pattern of sexual dimorphism while the Asian specimens do not. In figure 6.10A, African specimens are separated more on axis II than on axis I, the pongid pattern, but for the Asian specimens the reverse is the case. This could provide support for the separation of these groups on a subspecific if not a specific level, but obviously more evidence is needed to substantiate this claim (eg. Wood 1990). Thus future work could be directed toward an investigation of this apparent difference in patterns of sexual dimorphism within regional samples of *H. erectus*.

The CVA reinforces the PCA regarding patterns within *H. habilis*, where KNM-ER 1805 displays peculiarities of the mandibular and basal regions. It also points out the affinities of KNM-ER 1470 with African *H. erectus*, especially KNM-ER 3733. Its separation from the other *H. habilis* specimens could be due to sexual differences or to its greater cranial capacity, but not to this alone since the reallocation procedure using facial characters assigned this specimen to African *H. erectus*.

Within *A. africanus*, the greater prognathism of STS 5 relative to the other specimens causes considerable variability in the palatal and facial CVA's. Although STS 5 is commonly referred to as female, the palate PCA indicates that STS 5 should be a male if *A. africanus* follows a pongid pattern of sexual dimorphism. Analyses in other regions of the skull indicate, however, that STS 5 could be a female.

The robust australopithecines are distinguished from most other hominids in the palatal and mandibular CVA's due to their larger molars. The face CVA (axis III) provides some support for Williams (1984) claim that the OH 5 face should be realigned. On axis II (face CVA) *A. boisei* does not follow the *Gorilla* pattern of sexual dimorphism which is interesting since the degree of sexual dimorphism in *A. boisei* is often compared (as it is in this study) with that in *Gorilla*. This underlines the need for care when making comparisons between modern and fossil groups and the need for more research into the patterns of both fossil and pongid sexual dimorphism. Finally, in the base CVA, *A. boisei* and *H. erectus* show similarities in characters of width, but this is doubtless due to different functional requirements of both species in this region of the skull.

A. afarensis also has a different pattern of sexual dimorphism from that of *Gorilla* but in the mandibular and palate regions. The situation here is different to that for *A. boisei*. In the *A. boisei* sample, OH 5, KNM-ER 406, and KNM-ER 732 all have close scores while *Gorilla* males have higher scores than females. In the *A. afarensis* sample, females have higher values than males. So although the pattern of *A. afarensis* sexual dimorphism is different from that of *Gorilla*, this may be an indication of heterogeneity of the sample, rather than low dimorphism for these characters as in *A. boisei*, otherwise the sample size is too small to determine the significance of this phenomena. The palate CVA involves different specimens to the ones mentioned above, so while not illuminating the reason for such a pattern, does support the results of the mandibular analysis.

The reallocation procedure of the CVA is most successful in the face and regional combination regions (face: 88.2 %, regional combination 88 % correctly reclassified) where similarity between groups is less than the differences between them. Only two fossils are "misclassified": KNM-ER 1470 (African *H. erectus*, 1st choice; *H. habilis*, 2nd choice) in the face analysis and KNM-ER 732 (*Pan* female; *H. habilis*) in the regional combination analysis.

The mandibular (86 % correctly classified) and base (85.4 %) areas are the next most successful in allocating individuals to their original group. The base was more successful in that none of the fossil specimens is misclassified. In the mandible analysis, four fossil specimens are misclassified but for 3 out of 4 of these, the 2nd choice group is their original group (BK 67, A. L. 266.1, and the *A. afarensis* reconstruction). The 4th specimen, KNM-ER 730, is close to male *H. sapiens* and the Mauer mandible, possibly due to a number of estimated measurements made on this specimen.

In the palate analysis, 83.2 % of the specimens are correctly classified. Of the fossils, STW 73 (*Pan* female, 1st choice) and STS 53 (*H. habilis*) are misclassified though their 2nd choice group was *A. africanus.*

Finally, the vault allocation procedure was most unsuccessful (78 %) because the shape of the vault in most pongids is very similar. In this analysis only the vault of *Gorilla* is distinguished on some axes from those of the other pongids. Since all the fossils were assigned to their original group this pongid pattern of similarity between groups does not cause a problem, in other words, the vault proportions of the fossil hominid species are sufficiently different from one another to allow separation of these groups.

The allocation procedure can emphasise affinities between groups, for example KNM-ER 1470 and African *H. erectus* in the face and most pongids in vault region, or differences between individuals (eg. STS 53 and STW 73 in the palate). It also points out similarities between sexes, where males classify as females or *vice versa* in the modern groups, and may be useful in future studies of sexual patterns in fossil morphology.

6.5 Summary and Conclusions

6.5.1 Summary

The PCA and CVA both use a combination of variables to discriminate between individuals (PCA) and groups (CVA). The PCA is used to compare the fossils with a highly sexually dimorphic modern group in order to assess sex and homogeneity of the sample. PCA maximises within group variation and minimises between group variation so individuals most similar to one another will group together with those more different to one another "pushed" apart and the PCA allows some discussion of why this occurs. Finally, the homogeneity of fossil groups needs to be assessed in order to perform the CVA.

The CVA minimises the within group variation and maximises the between group differences. Fossil groups are defined using the results of the PCA to ensure that within group variability will be as low as possible. Using CVA one can discuss group similarities and differences in functional/ biological terms and it also allows an assessment of sexual dimorphism and of the homogeneity of groups.

6.5.2 Conclusions

This chapter demonstrates a number of trends within the fossil species, some of which indicate differences in patterns of sexual dimorphism and others implying heterogeneity of samples. It has shown the likely sex of a number of specimens, in some cases reinforcing current sex allocations, in others individuals not previously assigned to either sex. It has raised questions about patterns of hominoid sexual dimorphism (in *A. boisei* and *A. afarensis* as mentioned above) and about the homogeneity of some fossil samples, that is *H. erectus*, and *A. afarensis*. For *H. erectus*, evidence suggests regional and /or temporal differences between the African and Asian samples and between these and the Mauer mandible. For *A. afarensis*, the evidence is not so clear cut. Some specimens may belong to *A. afarensis*, such as A. L. 198.1, 266.1, and 288.1, while others, such as LH 4 and 333w.60, if not *A. afarensis* belong to some or other unidentifiable group.

This chapter has used the patterns of sexual dimorphism and variability within modern species 1) to place limits on the amount of variability within fossil species and thus assess the homogeneity of these species; and 2) to assess the extent and patterns of sexual dimorphism within fossil species in different cranial regions and to distinguish individual fossils by sex. The results of this chapter have raised questions which could provide avenues for future research on hominoid variability and patterns of sexual dimorphism.

CHAPTER 7: CLADISTIC ANALYSIS

7.1 Introduction

The analyses presented in the previous chapters provide an understanding of the patterns of character variability in the extant hominoids and allow the original data set to be divided into two subsets. The first includes variables found to be non-variable and non-dimorphic within the extant hominoids, and the second includes characters known to be variable and dimorphic within hominoids. Until recently, no assessment of character variation within populations has been considered prior to the use of these characters in cladistic analyses. With the knowledge of such variation within the extant hominoids I compare the results of using the subsets of my data, mentioned above, in separate cladistic analyses. This analysis is not concerned with the extraction of phylogenetic information. Instead, I hope to determine which of the two subsets of data provide the more parsimonious trees. Other aims of this study are to examine the result of combining the two subsets and also to assess the coding method used to transform the original data into discrete character states. The results are presented in section 7.2 along with a more detailed discussion of the above aims.

7.2 The Present Study

7.2.1 Introduction

Using the knowledge of patterns of character variation in the extant hominoids I wish to determine the validity of using variable traits in cladistic analyses. To do this I compare the results of using a) non-variable traits b) variable traits c) both types of traits in cladistic analyses in order to assess a) the ability of the two types of variables to group the sexes of the extant hominoids and b) which of of the two sets of variables provide the more parsimonious trees.

The most parsimoneous tree is one with the shortest length and highest consistency index. The length refers to the number of character state changes made from the root of the tree to its terminal branches while the consistency index (CI) is a measure of homoplasy; the lower the value of CI, the greater number of changes, including reversals which have had to be made and the highest value of CI is 1.00. Thus the most parsimoneour tree is one which requires the minimum number of character state changes.

During the preparation of the data for analysis, I found myself questioning the objectiveness of the coding method (outlined in Chapter 4) to transform the size standardised (logged) data into discrete character states. I wanted to determine how dependent the results of the cladistic analyses were on the coding method. As stated in Chapter 4, coding of data is done to maximise the amount of difference between characters. The coding involves the use of a constant which is derived 'empirically' (see Chapter 4). If the same constant is used to code both variable and non-variable data sets, important phyletic information may be lost since the constant most appropriate for one data set may not be for both. In order to ensure that both data sets are appropriately coded, the data sets of variable and non-variable traits are converted into discrete character states using different constants, where the constant for the variable traits is the larger of the two. In subsequent analyses the non-variable data set coded in this way will be referred to 'non-variable traits - own constant'.

In order to test the hypothesis that important information might be lost if only one constant is used, I assign the non-variable traits a second set of discrete character states. For this second set of non-variable character states, the variable trait constant is used in the coding method and this set of character states is referred to in subsequent analyses as 'non-variable traits - recoded'.

By assigning two sets of character states to the non-variable traits I attempt to determine how dependent the analyses are on the constant used in the coding of the data. Thus *two sets* of non-variable character states are used in *separate* cladistic analyses to determine which produce the more parsimonious trees (Section 2 of this study).

I also perform cladistic analyses where the variable and non-variable traits are combined into one data set. In these analyses, traits will have been coded into character states using either a 'different' constant or the 'same' constant. Thus I include the variable traits with non-variable traits (own constant) in one analysis, and with non-variable traits (recoded) in a separate analysis to compare the results of both analyses to see if differences arise.

The present study is divided into 4 sections. In the first section a test is made of the ability of both data sets to group together the sexes of the extant hominoids. If characters cannot distinguish between groups, or group together the sexes of the same species, then their utility in any analysis of taxonomic affiliations is questionable. In Section 1A the results of using non-variable traits (own constant) are analysed and in Section 1B the results of using variable traits are examined.

Section.2 is divided into two parts. Section 2A involves an analysis of the fossil hominids using non-variable traits (own constant) and in Section 2B non-variable traits (recoded) are used in the cladistic analyses. In Section 3 the results of using variable traits in cladistic analyses are presented. In Section 4 the two data sets are combined, but in Section 4A a different constant is used to code the two data sets, and in Section 4B the same constant is used to code the two data sets.

In Section 2, 3, and 4 the same 5 steps are followed. First, using 'combined' character states of the hypothetical ancestor (determined using the method outlined in Chapter 4), PAUP's MULPARS option is used to find a short tree. The MULPARS option allows a search for multiple, equally parsimonious, trees by swapping branches. It is used to find the tree with the shortest length. Since there may be more than one tree of this length, PAUP's branch and bound method is used since it finds all the most parsimonious trees. It is used to find all the shortest trees and those slightly longer (usually within three steps longer than the shortest tree) which yield between 8 and 15 trees per analysis. Only the most parsimonious tree(s) (the shortest tree(s) with the highest value(s) of CI) are be discussed in Sections 2, 3, and 4, the overall pattern of the longer trees are reviewed in the concluding Section.

Since the use of hypothetical ancestral character states may affect the internal arrangement of the ingroup taxa, the hypothetical ancestor is deleted and the most parsimonious tree is found for the ingroup taxa alone. The tree is rooted by placing *A. afarensis* as the sister group to all other hominids, thus making the assumption that *A. afarensis* is the most primitive hominid.

The third step involves deleting characters which are poorly resolved within the shortest tree(s). This is done to test the stability of the most parsimonious cladogram to see if the deletion of these characters cause a different arrangement of clades to take place. Characters which are poorly resolved within a tree have a CI of .5 or less (since the highest value of CI is 1.00, I decided to rate characters with CI values of .5 or less as being poorly resolved). The consistency index (CI) for a single character is the minimum possible number of changes divided by the actual number of changes (length) for that character (Swofford 1985).

The fourth step involves using different character states for the hypothetical ancestor (new ancestor). These character states are chosen from the outgroup node of one of the topologies mentioned in Chapter 4. The choice of topology is based upon its length and CI, the shortest tree with the highest CI being utilised. Once again the shortest tree(s) are found using the MULPARS option followed by the branch and bound option.

The fifth step, like the third step, involves the exclusion of characters with CI values of .5 or less from the construction of the shortest tree(s) for the same reason as stated previously.

Thus for each of Sections 2, 3, and 4, five analyses are performed: Part 1: the 'combined' ancestor is used to find the shortest tree(s); the 'combined' ancestor is deleted and *A. afarensis* is used to root the tree; poorly resolved characters are deleted; and Part 2: a 'new' ancestor is used to find the shortest tree(s); and finally, poorly resolved characters are deleted. In Section 2 (non-variable traits) and 4 (combined data sets), this procedure is followed twice in order to examine the effects of using different constants to code the non-variable traits.

In all Sections the MINF optimisation option (defined in Chapter 4) is used to determine the character states which define the internal nodes of the most parsimonious ingroup cladogram(s). These nodes are labelled 14 to 9 in figure 7.01, for example. The character state changes are read from the left to right on the tree so that character state changes at any one node are the differences between its character states and those at the preceeding node. These character state changes are synapomorphies (shared derived characters) which define a monophyletic group whose common ancestor is represented by the node. The definitions of each character can be used to interpret the biological nature of the changes and character state changes are referred to in terms of an increase or decrease in relative size of anatomical structures with reference to the average primate (also defined in Chapter 4).

The basal node of the ingroup cladogram is not discussed because the character state changes are affected by the choice of the outgroup which, in section one, is *Pongo*, and in sections 2, 3, and 4, are conservative estimates of the ancestral states.

In the final section of this chapter, the discussion section, I summarise the findings of the sections previous to it, and make concluding remarks.

7.2.2 Section 1A: Non-variable Traits

The character states of each sex of *H. sapiens*, *Pan*, *Gorilla*, and *Pongo* are listed in Table 7.01. Nine trees are generated at 156 steps or less and the same trees occur regardless of which sex of *Pongo* is at the root (see figure 7.01 for the shortest tree and Appendix 5 for all other, longer trees). The shortest tree (L=152; CI=.77) shows *Pongo* male (or female) leading to *Pongo* female (or male) which leads to a line which splits into *Gorilla* male and female on the one hand and *Pan* male on the other. *Pan* male shares a common ancestor with the line leading to *Pan* female and *H. sapiens.* A single extra step (L=153) and a slight decrease in CI (.765) gives a tree where the sexes of each species form sister groups to one another.

TABLE 7.01: NON-VARIABLE TRAITS: CHARACTER STATES BY SEX OF THE EXTANT HOMINOIDS

SP	SEX	M9	P2	P4	P5	P6	B1	B2	B4	B5	B6	B8	B9	B18	V1	V2	V8	V9	V10	F1	F4	F17
H.S.	M	3	2	0	0	0	3	3	4	6	6	2	5	2	8	7	8	7	8	2	0	0
H.S.	F	3	1	0	0	0	4	3	4	5	5	2	6	1	8	8	8	7	8	2	0	0
PAN	M	4	6	5	5	5	5	5	3	4	3	5	4	3	5	4	0	3	2	6	5	5
PAN	F	4	6	6	6	6	4	5	2	3	3	5	4	2	6	5	0	3	1	5	5	4
GO	M	3	3	5	8	5	3	5	4	2	3	5	3	7	0	0	2	2	0	7	5	8
GO	F	5	3	5	8	5	4	4	4	2	2	6	4	5	1	2	2	2	1	5	6	7
PO	M	5	6	7	8	7	4	3	4	4	5	3	2	6	0	1	1	3	0	2	7	6
PO	F	5	5	6	8	6	6	5	5	4	4	3	3	6	1	3	1	3	0	1	7	5

M9-External alveolar breadth
P2-Internal alveolar breadth
P4-External alveolar breadth
P5-Arcade length
P6-Arcade breadth
B1-Foramen magnum length
B2-Foramen magnum breadth
B4-Bistylomastoid width
B5-Bistyloid width
B6-Bicarotid canal width
B8-Biforamen ovale width
B9-Biinfratemporal fossa width
B18-Bimastoid breadth
V1-Frontal breadth
V2-Biparietal breadth
V8-Occipital chord
V9-Basi-bregmatic height
V10-Supraglabella-bregma chord
F1-Biorbital breadth
F4-Orbit height
F17-Bizygomatic tubercle breadth

FIGURE 7.01: SHORTEST TREE: NON-VARIABLE TRAITS: SEXES OF HOMINOIDS

```
                                                            H.s. M
                                                             ** 1
                       **************************************9
                     *10                                     ***2
                     * *                                   H.s. F
               *****11 ***** 4 Pan F
               *     *
       *******13     ***** 3 Pan M
       *       *
       *       *     ******** 5 Go M
******14       *****12
*      *             **** 6 Go F
*      *
*      *** 8 Po F
*
* 7 Po M
```

L=152 CI=.770

FIGURE 7.02: SHORTEST TREE: VARIABLE TRAITS: SEXES OF HOMINOIDS

```
                                                       H.s. M
                                                         ** 1
                              ***************************9
                      *******11                          ********2
                      *       *                            H.s. F
                  ***12       ************** 5 Go M
                  *   *
                  *   * **** 3 Pan M
       **********13   *10
       *          *     **** 4 Pan F
******14          *
*      *          ******* 6 Go F
*      *
*      ***** 8 Po F
*
* 7 Po M
```

L=125 CI=.744

In all nine trees *H. sapiens* and *Pan* share a common ancestor but with one tree (L=156; CI=.75) *Pan* and *Gorilla* share an ancestor which in turn shares an ancestor with *H. sapiens.* In two trees (L=154, CI=.76; L=156, CI=.75) *Pongo* males and females are not grouped together but there are trees of equal length and CI where this does happen. In all trees the sexes of *Pan* and *Gorilla* are depicted as either sharing a common ancestor (6/9 cases) or with one sex as common ancestor to the other (3/9 cases). In 2 out of those three cases *Pan* females share an ancestor with *H. sapiens* and in another 2 of three cases *Gorilla* females share a common ancestor with the line leading to *Pan* and *H. sapiens.* Thus 7/9, or 78 per cent, of the trees consistently group together the sexes of the same species in clades or in sister groups with one another.

Deletion of Characters

The deletion of M9 and B2, which have low individual CI's (.5 or less), results in a tree (L=143, CI=.79) identical to the shortest tree described above.

Character State Changes

The character state changes of the internal nodes of figure 7.01 are listed in Table 7.02. Node 13, the sister group of *Pongo*, describes the differences between the African apes and *H. sapiens* from *Pongo* and include a decrease in breadth of the mandible and palate; a decrease in some posterior basal elements and increase in anterior basal elements; an increase in frontal size; and changes to the orbit area.

Node 12 is a clade that contains *Gorilla* males and females and is defined by characters which separate them from *Pan* and *H. sapiens.* Changes include a further reduction of the breadth of the palate; a decrease in mid-basal structure width; a decrease in biparietal breadth and basi-bregmatic height but an increase in the size of the occipital area; and a widening of the face.

Node 11 is the sister group to *Gorilla* males and females including both sexes of *Pan* and *H. sapiens* and is defined by a decrease in the length of the palate arcade; a decrease in bimastoid breadth; and an increase in the breadth of the frontal and parietal bones.

Node 10 is the sister group to *Pan* males including *Pan* females and *H. sapiens* which have the following character state changes: a decrease in bimastoid breadth; an increase in frontal and parietal breadth; and a decrease in the width of the mid-face.

Node 9 is the sister group of *Pan* females and is a clade containing *H. sapiens* males and females. A large list of changes defines this node, not suprising considering

TABLE 7.02: CHARACTER STATE CHANGES: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMIOIDS

Key:	
M1 -	Increase in character M1 by one character state
M1(2)	Increase in character M1 by two character states
M1	Decrease in character M1 by one character state
M1(2)	Decrease in character M1 by two character states

NODE 13 ALL HOMINOIDS EXCEPT PONGO

M9	decrease in external alveolar breadth
P4	decrease in external alveolar breadth
P6	decrease in arcadal breadth
B6	decrease in bicarotid canal width
B8(2)	increase in biforamen ovale width
B9	increase in biinfratemporal fossa width
B18	decrease in bimastoid breadth
V10	increase in supraglabella - bregma chord
F1(3)	increase in maximum breadth of orbits
F4(2)	decrease in orbit height

NODE 12 GORILLA MALES AND FEMALES

P2(2)	decrease in internal alveolar breadth
B5(2)	decrease in bistyloid breadth
V2	decrease in biparietal breadth
V8	increase in occipital chord
V9	decrease in basi-bregmatic height
F17(2)	increase in bizygomatic tubercle breadth

NODE 11 PAN AND H. SAPIENS

P5(2)	decrease in arcadal length
B18(2)	decrease in bimastoid breadth
V1(4)	increase in frontal breadth
V2	increase in biparietal breadth

NODE 10 PAN FEMALES AND H. SAPIENS

B18	decrease in bimastoid breadth
V1	increase in frontal breadth
V2	increase in biparietal breadth
F17	decrease in bizygomatic tubercle breadth

NODE 9 H. SAPIENS

M9	decrease in external breadth
P2(3)	decrease in internal breadth
P4(5)	decrease in external breadth
P5(6)	decrease in arcadal length
P6(5)	decrease in arcadal breadth
B2(2)	decrease in foramen magnum width

TABLE 7.02: CHARACTER STATE CHANGES: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMIOIDS CONTINUED

NODE 9 CONTINUED

B5	increase in bistyloid breadth
B6(2)	increase in bicarotid canal width
B8(3)	decrease in biforamen ovale width
B9	increase in biinfratemporal breadth
V1(2)	increase in frontal breadth
V2(2)	increase in biparietal breadth
V8(7)	increase in occipital chord
V9(4)	increase in basi-bregmatic height
V10(7)	increase in supraglabella - bregma chord
F1(3)	decrease in biorbital breadth
F4(5)	decrease in orbit height
F17(4)	decrease in bizygomatic tubercle breadth

the differences between *Pan* and *H. sapiens*. These changes include an overall decrease in aspects of the mandible and palate; a decrease in the width of the foramen magnum and of the distance between the foramen ovales, along with an increase in bistyloid breadth, bicarotid canal width, and biinfratemporal fossa width. In the vault, the changes include overall increase in size and in the face a decrease in upper and mid-face breadth and in orbit height.

Thus the features which link *H. sapiens* with *Pan* include an increase in vault size, narrowing of the mid-face (*Pan* females), decrease in bimastoid breadth, and a decrease in palate arcadal length.

Summary

Overall, the non-variable traits place the sexes as either sister groups to one another or in an ancestral/ descendant relationship. In the two cases that this does not occur there are trees of equal length and CI where this relationship holds.

7.2.3 Section 1B: Variable Traits

The variable character states for each sex of *H. sapiens*, *Pan*, *Gorilla*, and *Pongo* are listed in table 7.03. Ten trees are generated at 128 steps or less; the trees being the same regardless of whether *Pongo* males or females are used a the root (see figure 7.02 for the shortest tree and Appendix 5 for all trees of longer length). The shortest tree (L=125, CI=.744) is slightly shorter, but with a slightly lower CI, than the shortest non-variable tree. In all ten cases the sexes of *H. sapiens* share a common ancestor. *Pan* males and females share a common ancestor in 5 cases and in 4 cases there is a direct evolutionary relationship. In one case *Gorilla* females occupy an intermediate position between *Pan* females and males (L=128, CI=.727).

In 7/10 cases *Gorilla* males share a common ancestor with *H. sapiens*. In two cases (2/7) *Gorilla* males and females are in a direct evolutionary relationship with *Gorilla* females sharing a common ancestor with the ancestor of *Gorilla* males. In 3 cases (3/7) the *Gorilla* sexes are separated by *Pan* and in one case by *Pan* males alone. In one case *Gorilla* females, *Pan*, and the ancestor of *Gorilla* males share a common ancestor.

The other three cases are more complicated. In one case *H. sapiens* shares a common ancestor with the ancestor of *Gorilla* males, *Gorilla* males share the common ancestor of *Gorilla* females, and they in turn share a common ancestor with *Pan* (L=128, CI=.727). Another tree of the same length and CI shows *Pan* and *Gorilla* sharing a common ancestor which in turn shares a common ancestor with *H. sapiens*

TABLE 7.03: VARIABLE TRAITS: CHARACTER STATES
BY SEX OF THE EXTANT HOMINOIDS

SP	SEX	M5	M7	M10	M11	P1	P7	P8	B10	B13	B19	V11	V12	V13	V14	V17	V20	F2	F5	F12	F13	F21
H.S.	M	3	2	4	3	0	3	3	2	5	4	8	8	4	4	5	3	6	0	2	1	1
H.S.	F	1	2	2	2	0	3	2	2	4	4	8	8	5	5	5	3	7	0	2	1	1
PA	M	4	3	4	4	5	4	4	5	4	4	0	0	2	3	5	5	6	8	5	4	4
PA	F	4	4	4	4	5	4	4	5	4	3	1	0	3	3	5	5	5	5	5	4	5
GO	M	3	3	3	3	5	3	3	4	4	3	0	4	6	6	2	4	3	8	4	5	5
GO	F	4	5	4	4	5	4	5	5	4	4	0	0	4	4	3	4	2	8	5	6	4
PO	M	6	6	5	6	5	6	6	4	4	5	0	0	3	3	3	5	1	0	5	4	6
PO	F	6	7	6	6	5	5	4	5	3	5	0	0	4	4	4	5	0	0	4	4	4

M5-Symphyseal height
M7-Corpus thickness
M10-Depth at M1
M11-Depth at M3
P1-Palate length
P7-Depth at M1
P8-Depth at M3
B10-Tympanic - carotid canal chord
B13-Biforamen ovale line - bitympanic line
B19-Nuchal crest width
V11-Inion chord
V12-Inion arc
V13-Nuchal chord
V14-Nuchal arc
V17-Biporionic breadth
V20-Porion - zygomaxillare chord
F2-Inter-orbital breadth
F5-Glabella projection
F12-Upper facial height
F13-Nasal height
F21-Cheek height

(same as the non-variable tree where L=156 and CI=.75). The third case (L=127, CI=.732) shows *Gorilla* sharing a common ancestor with *Pan* males which in turn share a common ancestor with *Pan* females which share a common ancestor with *H. sapiens.* Thus the sexes are correctly sorted into clades or sister groups in 4/10 or 40 per cent of the trees.

Deletion of Characters

The deletion of characters V14, V17, and F5 results in two trees (L = 95, CI = .832), one identical to the shortest tree described above, and a second where the sexes of *Pan* are ancestral to one another and not sister groups (see Appendix 5 for trees).

Character State Changes

The character state changes of the internal nodes of figure 7.02 are listed in Table 7.04. Node 13 is defined by characters which distinguish the African apes and *H. sapiens* from *Pongo.* These character state changes include a decrease in the height and thickness of the mandible and a slight decrease of the palate depth; a decrease in nuchal crest width; an increase in inter-orbital breadth; and a large increase in the size of glabella.

Node 12 is the sister group of *Gorilla* females and is defined by a decrease in mandibular corpus thickness; an increase in biporionic breadth; and a large increase in inter-orbital breadth.

Node 10 is a clade which includes both sexes of *Pan* and *H. sapiens* which is defined only by a decrease in nuchal area.

Node 11 is the sister group of *Pan* and includes *Gorilla* males and *H. sapiens.* The changes taking place at this node include a decrease in the depth of the mandible and palate; a decrease in the tympanic-carotid canal chord; an increase in inion arc; and a shortening of the height and length of the face.

Node 9 contains the clade of *H. sapiens* and is defined by a decrease in proportions of the mandible and palate; a further decrease in the chord between the tympanic and carotid canal; a very large increase in occipital area and changes involved in the restructuring of the human face.

The symplesiomorphic characters which link male *Gorilla* and *H. sapiens* can be found in Table 7.04, Node 11. An increase in inion chord relative to the standard primate is caused by cranial expansion of the occipital in *H. sapiens* but in male

TABLE 7.04: CHARACTER STATE CHANGES: VARIABLE TRAITS: SEXES OF EXTANT HOMINOIDS

Key: M1 - Increase in character M1 by one character state
M1(2) Increase in character M1 by two character states
M1 Decrease in character M1 by one character state
M1(2) Decrease in character M1 by two character states

NODE 13 ALL HOMINOIDS EXCEPT PONGO

M5(2)	decrease in symphysis height
M7	decrease in corpus thickness
M10	decrease in depth at M1
M11(2)	decrease in depth at M3
P7	decrease in depth at M1
B19	decrease in nuchal crest width
F2	increase in interorbital breadth
F5(5)	increase in glabella projection

NODE 12 PAN, GORILLA MALE, H. SAPIENS

M7(2)	decrease in corpus thickness
V17	increase in biporionic breadth
F2(3)	increase in interorbital breadth

NODE 10 PAN

V13	decrease in nuchal chord
V14	decrease in nuchal arc

NODE 11 GORILLA MALE AND H. SAPIENS

M5	decrease in symphysis height
M11	decrease in depth at M3
P7	decrease in depth at M1
P8	decrease in depth at M3
B10	decrease in tympanic- carotid canal chord
V12(4)	increase in inion chord
V20	decrease in porion-zygomaxillare chord
F12	decrease in upper facial height

NODE 9 H. SAPIENS

M7	decrease in corpus thickness
P1(5)	decrease in internal alveolar breadth
B10(2)	decrease in tympanic-carotid canal chord
V11(8)	increase in inion chord
V12(4)	increase in inion arc
V20	decrease in porion-zygomaxillare chord
F2	increase in interorbital breadth
F5(5)	decrease in glabella projection
F12(2)	decrease in upper facial height
F13(3)	decrease in nasal height
F21(3)	decrease in cheek height

Gorilla, is due to the expansion of this area in conjunction with the development of the nuchal crest. A decrease in facial height and length in male *Gorilla* may be due to the tilting upwards of the face which occurs after the initial downward and forward growth (Krogman 1931abc). Thus the length and height of the face of male *Gorilla* is relatively shorter than the standard primate, whereas that of *H. sapiens* is absolutely shorter. The reduction in size of the mandibular and palatal characters in male *Gorilla* may be caused by the necessity of accomodating such large canines. Finally, the reduction in the tympanic-carotid canal chord in both *H. sapiens* and male *Gorilla* may be a true symplesiomorphic traits or a parallel / convergent trait.

Summary

Thus overall, *Gorilla* males align most closely with *H. sapiens* and the affiliation of the sexes with their own species partner is not consistent when variable traits are used.

Discussion

Variable characters provide trees of short length and high CI but do not consistently place female *Pan* and *Gorilla* with their conspecific males (only in 40 per cent of the trees does this happen). Overall, *Gorilla* males are depicted as the closest in relation to *H. sapiens.* Thus trees based on such characters do not effectively sort the extant hominoids.

Non-variable characters provide trees of longer length but slightly higher CI's than those of the variable characters. The sexes are more consistently aligned with one another, either as sister groups, or sharing common ancestry (in 78 per cent of the trees) and *Pan* is depicted as the closest in relation to *H. sapiens.*

In both analyses there is one cladogram showing *Pan* and *Gorilla* as a monophyletic group as a sister clade with *H. sapiens* and thus the trichotomy of *H. sapiens*, *Pan*, and *Gorilla* is not resolved by these analyses.

Since these characters have been standardised for size the character state changes describe changes in size relative to the average primate. This means that males and females of a species can still demonstrate dimorphism in their size relative to that primate. In species that are highly size or shape dimorphic, variable characters are likely to provide a larger number of possible trees/cladograms/scenarios than are non-variable traits by reason of their very nature.

7.2.4 Section 2A: Non-variable traits: Own constant

Part 1

The data used in this section can be found in Table 7.05. In the first analysis, fifteen trees of 178 steps or less are generated using the branch and bound option (See Appendix 5) and using a hypothetical ancestor possessing the most predominant states (combined ancestor) (see introduction for explanation). The shortest tree (L=175, CI=.657) is seen in figure 7.03.

Deletion of Hypothetical Ancestor

The deletion of the ancestral taxon results in a tree (L=155, CI=.723) identical to the one in figure 7.03 except *A. afarensis* becomes the root of the tree (no characters have an individual CI of .5 or less).

Character State Changes

The character state changes and their associated nodes which are discussed in this section refer to those found in figure 7.03 (see table 7.06 for a list of character state changes at each node).

Node 10 is part of a clade containing *A. afarensis* and *A. boisei* and is defined by a reduction in internal alveolar breadth (P2) and increases in the width of anterior and mid-basal structures.

Node 13 contains all hominids except *A. afarensis* and *A. boisei* and is defined by increases in proportions of the vault.

Node 12 is sister group to a clade containing *A. africanus* and consists of *H. habilis/ A. robustus* and *H. erectus/ H. sapiens.* It is defined by only a few isolated characters: a decrease in palate length; an increase in frontal breadth; and a decrease in orbit height.

Node 11 is a clade containing *H. habilis/ A. robustus* which is defined by a widening of the palate; a reduction in width of mid- and anterior basal elements; an increase in the biorbital breadth; and an increase in mid-facial width.

Node 9 is a sister group to Node 11 and consists of a clade of *H. erectus* and *H. sapiens.* It is defined by a reduction in palate proportions; a decrease in foramen magnum width; an increase in vault proportions; a decrease in orbit height; and a narrowing of the mid-face.

TABLE 7.05: NON-VARIABLE TRAITS: CHARACTER STATES (OWN CONSTANT)

SP	M9	P2	P4	P5	P6	B1	B2	B4	B5	B6	B8	B9	B18	V1	V2	V8	V9	V10	F1	F4	F17
OUTGP1	4	3	5	5	5	4	4	4	4	3	3	3	2	1	2	1	3	1	2	5	4
OUTGP2	4	3	5	8	5	4	4	4	4	3	3	3	6	1	2	1	3	1	2	6	6
H.S.	3	2	0	0	1	3	3	4	5	5	3	5	2	8	7	8	7	8	2	0	0
A.AFAR	4	1	4	4	3	5	5	5	6	8	6	8	4	0	2	2	1	9	3	3	9
A.AFRIC	7	2	5	4	4	4	4	4	5	5	5	3	4	2	3	3	5	5	3	3	5
A.ROB	9	5	8	2	7	9	9	1	4	3	1	6	7	3	9	9	9	0	8	1	7
A.BOIS	4	1	8	4	7	0	5	5	6	5	7	7	6	3	1	0	2	0	5	2	5
H.HAB	5	2	7	1	6	4	4	3	4	4	2	6	3	4	3	7	1	4	5	1	6
H.ER	4	4	5	0	3	4	3	5	6	5	6	7	3	4	5	3	1	5	4	0	2

OUTGP1= COMBINATION ANCESTOR
OUTGP2= TOPOLOGY (4(3(1,2))) (L=108 CI=.880)
WHERE 1=HS, 2=PA, 3=GO, 4=PO

M9-External alveolar breadth
P2-Internal alveolar breadth
P4-External alveolar breadth
P5-Arcade length
P6-Arcade breadth
B1-Foramen magnum length
B2-Foramen magnum breadth
B4-Bistylomastoid width
B5-Bistyloid width
B6-Bicarotid canal width
B8-Biforamen ovale width
B9-Biinfratemporal fossa width
B18-Bimastoid breadth
V1-Frontal breadth
V2-Biparietal breadth
V8-Occipital chord
V9-Basi-bregmatic height
V10-Supraglabella-bregma chord
F1-Biorbital breadth
F4-Orbit height
F17-Bizygomatic tubercle breadth

FIGURE 7.03: SHORTEST TREE: NON-VARIABLE TRAITS: OWN CONSTANT:
COMBINED ANCESTOR

```
* 1 OUTGROUP
*                                                           H.S.
*                                   ******************************2
*                        ***********9
*                        *          ********** 8 H.ER
*                    ***12
*                    *   *         ******************* 5 A.ROB
*              ****13    *********11
*              *    *              ******** 7 H.HAB
*              *    *
**************14    ************ 4 A.AFRIC
               *
               *       ********** 3 A.AFAR
               *******10
                       ******************** 6 A.BOIS
```

L=175 CI=.657

TABLE 7.06: CHARACTER STATE CHANGES: NON-VARIABLE TRAITS: OWN CONSTANT

Key:	M1 -	Increase in character M1 by one character state
	M1(2)	Increase in character M1 by two character states
	M1	Decrease in character M1 by one character state
	M1(2)	Decrease in character M1 by two character states

NODE 10 A.AFARENSIS + A.BOISEI

P2	decrease in internal alveolar breadth
B2	increase in foramen magnum width
B4	increase in bistylomastoid width
B5	increase in bistyloid width
B8(3)	increase in biforamen ovale width
B9	increase in biinfratemporal fossa width
B18	increase in bimastoid width

NODE 13 A.AFRICANUS, H.HABILIS, A.ROBUSTUS, H.ERECTUS, AND H. SAPIENS

V2	increase in biparietal breadth
V8	increase in occipital chord
V10(3)	increase in supraglabella-bregma chord

NODE 12 H.HABILIS, A.ROBUSTUS, H.ERECTUS, AND H. SAPIENS

P5(2)	decrease in arcadal length
V1	increase in frontal breadth
F4(2)	decrease in orbit height

NODE 11 H. HABILIS AND A. ROBUSTUS

P4(2)	increase in external alveolar breadth
P6(2)	increase in external arcadal breadth
B4	decrease in bistylomastoid breadth
B5	decrease in bistyloid breadth
B6	decrease in carotid canal breadth
B8	decrease in biforamen ovale width
F1(2)	increase in biorbital breadth
F17	increase in bizygomatic tubercle breadth

NODE 9 H.ERECTUS AND H. SAPIENS

P5(2)	decrease in arcadal length
P6	decrease in external arcadal breadth
B2	decrease in foramen magnum width
V1	increase in frontal breadth
V2(3)	increase in biparietal breadth
F4	decrease in orbit height
F17(3)	decrease in bizygomatic tubercle breadth

Deletion of Characters

The next step involves the deletion of 7 characters which have individual CI values of .5 or less including: P2 (maximum lingual breadth), B5 (bistyloid breadth), B8 (biforamen ovale breadth), B9 (biinfratemporal fossa breadth), B18 (bimastoid breadth), V8 (occipital chord), and V9 (basi-bregmatic height). The shortest tree (L=105, CI=.752); is only different from figure 7.03 by the position of *A. boisei* (see figure 7.04).

Part 2

In this analysis, a different set of character states is used for the hypothetical ancestor, those obtained from the most parsimonious tree; in this case one where *Pan* and *H. sapiens* form a clade as sister group with *Gorilla* with *Pongo* as ancestor (L=108, CI=.880). Thirteen trees are generated at 181 steps or less (see Appendix 5) with two shortest trees (L=179, CI=.665), one of which has the same arrangement of clades as figure 7.03 (see figure 7.05 for second tree).

Character State Changes

Character state changes of one of the shortest trees in this section (tree depicted in figure 7.03) are almost identical to those discussed in Part 1. The differences for this tree include: Node 10, B18 is removed and Node 9, B18 is added as a character state change. The character states listed in Table 7.06 are identical for all other nodes.

The second of the shortest trees (figure 7.05) has nodes defined slightly differently due to the placement of the clades on the tree. Thus Node 12 is the same as Node 11 of table 7.06 with the following differences: B5, B6, and F17 are lost and a decrease in arcadal length (P5(2)) and a decrease in orbit height (F4) are added as synapomorphies of this clade.

Node 13 is a clade consisting of *A. boisei*, *A. afarensis*, *A. africanus*, *H. erectus*, and *H. sapiens*, and is defined by a reduction in arcadal breadth (P5), an increase in width of the basal elements (B5, B6, B8 (2)) and a decrease in the width of the mid-face (F17).

Node 10 is virtually the same as Node 10 of Part 1 but is also defined by a decrease in vault proportions (V2, V8) but not by B18.

Node 11 consists of a clade containing *A. africanus*, *H. erectus*, and *H. sapiens*, defined only by an increase in frontal proportions (V4(4)).

FIGURE 7.04: SHORTEST TREE: NON-VARIABLE TRAITS: OWN CONSTANT
COMBINED ANCESTOR: CHARACTERS DELETED

```
* 1 OUTGRUP
*                                                          H.S.
*                                    ****************************2
*                          **********9
*                          *         *** 8 H.ER
*                *********12                              A.ROB
*                *         *                            *********5
*                *         *         ******************10
*             **13         *********11                  *********6
*             *  *                   *                    A.BOIS
*             *  *                   *** 7 H.HAB
*************14  *
              *  ***** 4 A.AFRIC
              *
              ************ 3 A.AFAR
```

L=105 CI=.752

FIGURE 7.05: SHORTEST TREE: NON-VARIABLE TRAITS: OWN CONSTANT: NEW ANCESTOR (TREE 2)

```
* 1 OUTGROUP
*                                                           H.S.
*                                    ****************************2
*                        ************9
*                     **11           ******* 8 H.ER
*                     *  *
*                ****13  ********** 4 A.AFRIC
*                *    *
*                *    *     ********** 3 A.AFAR
****************14    *****10
                 *          **************** 6 A.BOIS
                 *
                 *       ************** 5 A.ROB
                 *******12
                         ********** 7 H.HAB
```

L=179 CI=.665

Node 9 is defined by the same characters as in Part 1 except for V10.

Deletion of Characters

The final analysis involves the deletion of four characters with individual CI values of .5 or less: P2 (maximum lingual breadth), B5 (bistyloid breadth), B8 (biforamen ovale breadth), and B9 (basi-bregmatic height). The shortest tree (L=139, CI=.727) is found in figure 7.06.

Discussion

Parts 1 and 2 show that a deletion of characters provides a shorter tree of higher CI with movement of only one taxon. The use of a different ancestor provides trees of slightly longer length than in Part 1 but of higher CI, though one of the shortest trees of Part 2 (no characters deleted) has the same arrangement of clades as the tree in Part 1. The deletion of characters in Part 2 provides a tree of longer length and higher CI and it is most similar to the tree in Part 1 (characters deleted), though the position of the *A. robustus*/ *A. boisei* clade differs between the two trees (see figures 7.04 and 7.06).

The choice of ancestral states does not make a great deal of difference to the way each node is defined, with the same clades being defined by almost all the same characters. The use of a different ancestor does, however, lead to the production of two different shortest trees, the second of which (figure 7.06) is made up of, in parts, different clades to those found in figure 7.03. Thus the character state changes of this tree differ from those of figure 7.03. The characters deleted in Parts 1 and 2 are ones which define the *A. afarensis*/ *A. boisei* clade which would account for the repositioning of *A. boisei* in the shortest trees of these sections.

Overall, non-variable traits, coded in order to maximise the differences between characters, provide trees with CI's of less than .700. Only when characters are deleted does the CI reach higher levels. This may be due to the effect of the ancestral states since a tree rooted to *A. afarensis* has a CI of .723.

7.2.5 Section 2B: Non-variable traits: Recoded

Part 1

The character states used in this analysis are listed in table 7.07. Nine trees are generated at 129 steps or less using the combined hypothetical ancestral states (see Appendix 5). Two shortest trees (L=127 CI=.740) are depicted in figures 7.07a and b, the only difference being the relationship between *A. afarensis* and *A. boisei*.

FIGURE 7.06: SHORTEST TREE: NON-VARIABLE TRAITS: OWN CONSTANT:
NEW ANCESTOR: CHARACTERS DELETED

```
* 1 OUTGROUP
*                                                           H.S.
*                                          **********************2
*                                  ********9
*                       **********11       ****** 8 H.ER
*                       *          *
*                   ***12          ******** 7 H.HAB
*                   *   *
*            ******13   ***** 4 A.AFRIC
*            *      *
************14      ********** 3 A.AFAR
             *
             *             ************* 5 A.ROB
             *************10
                           *** 6 A.BOIS
```

L=139 CI=.727

TABLE 7.07: NON-VARIABLE TRAITS: CHARACTER STATES (RECODED)

SP	M9	P2	P4	P5	P6	B1	B2	B4	B5	B6	B8	B9	B18	V1	V2	V8	V9	V10	F1	F4	F17
OUTGP1	4	4	5	5	4	4	4	4	4	3	4	4	3	2	3	2	3	2	3	5	4
OUTGP2	4	4	5	7	4	4	4	4	4	3	4	4	5	2	3	2	3	2	3	5	5
H.S.	3	3	1	0	2	4	3	4	5	5	3	5	2	7	6	8	6	8	3	0	0
A.AFAR	4	2	4	4	4	5	5	4	6	8	5	8	4	1	3	2	2	9	3	3	9
A.AFRIC	6	2	5	4	4	4	4	4	5	5	5	3	4	3	3	4	4	5	3	3	5
A.ROB	9	5	7	2	6	9	9	2	4	4	2	5	6	4	9	9	9	0	7	2	6
A.BOIS	4	2	6	4	6	1	4	5	5	5	6	6	6	3	2	1	2	1	5	3	5
H.HAB	5	3	6	2	6	4	4	3	4	4	3	5	4	4	3	6	2	4	4	2	5
H.ER	4	4	4	0	3	4	3	5	5	5	5	6	4	4	5	4	2	5	4	1	3

OUTGP1= COMBINATION ANCESTOR
OUTGP2= TOPOLOGY (4(3(1,2))) (L=80 CI=.913)
WHERE 1=HS, 2=PA, 3=GO, 4=PO

M9-External alveolar breadth
P2-Internal alveolar breadth
P4-External alveolar breadth
P5-Arcade length
P6-Arcade breadth
B1-Foramen magnum length
B2-Foramen magnum breadth
B4-Bistylomastoid width
B5-Bistyloid width
B6-Bicarotid canal width
B8-Biforamen ovale width
B9-Biinfratemporal fossa width
B18-Bimastoid breadth
V1-Frontal breadth
V2-Biparietal breadth
V8-Occipital chord
V9-Basi-bregmatic height
V10-Supraglabella-bregma chord
F1-Biorbital breadth
F4-Orbit height
F17-Bizygomatic tubercle breadth

FIGURE 7.07A: SHORTEST TREE: NON-VARIABLE TRAITS: RECODED:
COMBINED ANCESTOR (TREE 1)

```
* 1 OUTGROUP
*                                                           H.S.
*                                  ******************************2
*                       ***********9
*                       *          ***** 8 H.ER
*                  ****11
*                  *    *        ***************** 5 A.ROB
*             ****12    ********10
*             *    *             **** 7 H.HAB
*            13    *
*            **    ******** 4 A.AFRIC
************14*
             ******************* 6 A.BOIS
             *
             ************* 3 A.AFAR
```

L=121 CI=.752

FIGURE 7.07B:SHORTEST TREE: NON-VARIABLE TRAITS: RECODED:
COMBINED ANCESTOR (TREE 2)

```
* 1 OUTGROUP
*                                                           H.S.
*                                 *******************************2
*                     ************9
*                     *           ******* 8 H.ER
*                 ***12
*                 *   *        ***************** 5 A.ROB
*            ****13   ********11
*            *    *            **** 7 H.HAB
*            *    *
************14    *********** 4 A.AFRIC
             *
             *   ************* 3 A.AFAR
             ***10
                 ***************** 6 A.BOIS
```

L=121 CI=.752

Deletion of Hypothetical Ancestor

The deletion of the ancestral taxon and the rerooting of the ingroup to *A. afarensis* results in a tree (L=113 CI=.796) having the same arrangement of clades as the trees in figure 7.07a. All characters in this tree have a CI of greater than .5.

Character State Changes

Character state changes for the tree in figure 7.07a are listed in table 7.08. Node 13 includes all hominids except *A. afarensis* and is defined only by an increase in frontal breadth.

Node 12 (Node 13 in figure 7.07b) is a monophyletic group consisting of *A. africanus*, *H. habilis*, *A. robustus*, *H. erectus*, and *H. sapiens*, and is defined only by increases in vault proportions.

Node 11 (Node 12 in figure 7.07b), a clade consisting of *H. habilis*, *A. robustus*, *H. erectus*, and *H. sapiens*, is defined by an increase in internal alveolar breadth (not in figure 7.07b, Node 12), a reduction in arcadal length, an increase in frontal breadth, and a decrease in orbit height.

Node 10 (Node 11 in figure 7.07b) is a clade consisting of *H. habilis* and *A. robustus* which is defined by an increase in palate breadth, a reduction in width of basal structures, and an increase in biorbital breadth.

Node 9 of both trees consists of the *H. erectus*/*H. sapiens* clade which is defined by a decrease in palate proportions, a decrease in foramen magnum width, an increase in vault proportions, a decrease in orbit height, and a decrease in mid-facial width.

Deletion of Characters

Only one character has a CI of .5 or less (P2, internal breadth) when the character states of the combined ancestor are used. Its deletion results in shortest trees (L=121 CI=.752) which have the same arrangement of clades as the trees in figure 7.07a and b.

Part 2

When determining ancestral states, the topology with the shortest length and highest CI (L=80 CI=.913) is one in which *Pan* and *H. sapiens* are sister groups forming clade which is sister group to a clade containing *Gorilla*. Using the character states from the outgroup node of this tree as those of the hypothetical ancestor, results in 13 trees of 130 steps or less (see Appendix 5). There are 3 shortest trees (L=128 CI=.750), two having the same arrangements of clades as those in figures 7.07a and

TABLE 7.08: CHARACTER STATE CHANGES: NON-VARIABLE TRAITS: RECODED

Key:	
M1 -	Increase in character M1 by one character state
M1(2)	Increase in character M1 by two character states
M1	Decrease in character M1 by one character state
M1(2)	Decrease in character M1 by two character states

NODE 13 ALL TAXA BUT A.AFARENSIS

V1	increase in frontal breadth

NODE 12 A.AFRICANUS, H.HABILIS, A.ROBUSTUS, H.ERECTUS, H.SAPIENS

V8(2)	increase in occipital chord
V10(2)	increase in supraglabellar- bregma chord

NODE 11 H.HABILIS, A.ROBUSTUS, H.ERECTUS, H.SAPIENS

P2	increased internal alveolar breadth
P5(2)	decreased arcadal breadth
V1	increased frontal breadth
F4	decreased orbital height

NODE 10 A.ROBUSTUS, H.HABILIS

P4	increased external alveolar breadth
P6(2)	increase in external arcadal breadth
B4	decreased bistylomastoid breadth
B5	decrease in bistyloid breadth
B6	decrease in bicarotid canal width
B8(2)	decrease in biforamen ovale breadth
F1	increase in biorbital breadth

NODE 9 H.ERECTUS, H. SAPIENS

P4	decrease in external alveolar breadth
P5(2)	decrease in arcadal length
P6	decrease in external arcadal breadth
B2	decrease in formen magnum width
V2(2)	increase in biparietal breadth
V10	increase in supraglabella - bregma chord
F4	decrease in orbit height
F17(2)	decrease in bizygomatic tubercle breadth

b, and the third can be seen in figure 7.08. The only difference between the trees is the relationship between *A. afarensis* and *A. boisei.*

Character State Changes

The character state changes in the three shortest trees are almost identical to those listed in table 7.08. For the clades of *H. erectus/ H. sapiens*, *H. habilis/ A. robustus*, and of *H. habilis*, *A. robustus*, *H. erectus*, *H. sapiens*, the character state changes are the same (except Node 9 of tree 3 where F17 is not included). The clade containing *A. africanus*, *H. habilis*, *A. robustus*, *H. erectus*, *H. sapiens* is not defined by V10 in tree 1 but is identical to Node 12 for the other two trees. Node 13 for tree one (all but *A. boisei*) is defined by a reduction in bimastoid breadth (B18) and an increase in frontal size (V10(2)). Node 13 in tree 2 (all but *A. afarensis*) is defined by an increase in frontal size (V1). Node 10 of tree 3 (*A. afarensis/ A. boisei*) is defined by a decrease in internal alveolar breadth (P2) and an increase in width of some basal structures (B8, B9).

Deletion of Characters

Only one character has an individual CI of .5 or less (P2) and the deletion of this character results in three shortest trees identical in their arrangement of clades to those mentioned above (L=122 CI=.762).

Discussion

A comparison of Part 1 and 2 shows that a different ancestor provides trees of one extra step and slightly higher CI. The trees are virtually the same but the relationship of *A. afarensis* and *A. boisei* is not resolved. The deletion of one character in Part 1 and 2 does not resolve the *A. afarensis/ A. boisei* relationship, it only provides trees of slightly shorter length and higher CI. A comparison of the character state changes from Part 1 and 2 shows that the same clades are defined with virtually the same characters.

7.2.6 Section 3: Variable Traits

Part 1

Character states used in this analysis can be found in Table 7.09. In this analysis 9 trees are generated at 184 steps or less (see Appendix 5), with the shortest tree (L=180 CI=.617) depicted in figure 7.09.

Deletion of Hypothetical Ancestor

When the ancestral taxon is removed from the construction of the tree and

FIGURE 7.08: SHORTEST TREE: NON-VARIABLE TRAITS: RECODED:
NEW ANCESTOR (TREE 3)

```
* 1 OUTGROUP
*                                                          H.S.
*                                  *****************************2
*                       ************9
*                       *           ***** 8 H.ER
*                  ****11
*                  *    *         **************** 5 A.ROB
*                *12    *********10
*                * *              **** 7 H.HAB
*             **13 *
*             *  * ******** 4 A.AFRIC
*************14  *
              *  ************* 3 A.AFAR
              *
              **************** 6 A.BOIS
```

L=128 CI=.750

TABLE 7.09: VARIABLE TRAITS: CHARACTER STATES

SP	M5	M7	M10	M11	P1	P7	P8	B10	B13	B19	V11	V12	V13	V14	V17	V20	F2	F5	F12	F13	F21
OUTGP1	3	3	3	3	5	3	4	5	4	4	0	0	3	3	4	4	1	0	5	4	5
OUTGP2	3	4	3	3	5	3	4	5	4	3	0	0	3	3	4	4	1	0	5	4	5
H.S.	1	1	3	2	0	2	2	1	5	4	8	8	4	4	6	2	8	0	0	0	0
A.AFAR	3	8	5	3	5	0	0	1	2	2	5	3	1	0	6	8	8	8	1	0	2
A.AFRIC	2	8	5	2	5	4	4	7	4	4	8	8	0	0	3	6	6	4	3	2	5
A.ROB	4	8	4	2	2	1	4	4	6	9	9	9	9	9	3	7	8	8	2	1	4
A.BOIS	3	8	5	2	4	8	4	5	5	0	6	4	0	0	5	8	5	8	3	1	7
H.HAB	0	8	3	3	3	3	4	3	5	4	8	8	0	0	4	5	7	5	2	0	7
H.ER	2	6	4	4	0	4	0	2	3	5	8	8	0	2	6	3	7	7	1	0	6

OUTGP1= COMBINATION ANCESTOR
OUTGP2= TOPOLOGY (4(3(1,2))) (L=227 CI=.877)
WHERE 1=HS, 2=PA, 3=GO, 4=PO

M5-Symphyseal height
M7-Corpus thickness
M10-Depth at M1
M11-Depth at M3
P1-Palate length
P7-Depth at M1
P8-Depth at M3
B10-Tympanic - carotid canal chord
B13-Biforamen ovale line - bitympanic line
B19-Nuchal crest width
V11-Inion chord
V12-Inion arc
V13-Nuchal chord
V14-Nuchal arc
V17-Biporionic breadth
V20-Porion - zygomaxillare chord
F2-Inter-orbital breadth
F5-Glabella projection
F12-Upper facial height
F13-Nasal height
F21-Cheek height

FIGURE 7.09: SHORTEST TREE: VARIABLE TRAITS:
COMBINED ANCESTOR

```
* 1 OUTGROUP
*                                                              H.S.
*                                             ********************2
*                                   **********9
*                               ***12         ********* 8 H.ER
*                               *   *
*                          ****13   ***** 7 H.HAB
*                          *    *
*                          *    ********* 4 A.AFRIC
**************************14
                           *        **************** 3 A.AFAR
                           *   ****10
                           ***11    ***** 5 A.ROB
                               *
                               ********** 6 A.BOIS
```

L=180 CI=.617

A. afarensis placed as the root, the resulting tree (L=137 CI=.693) is depicted in figure 7.10. Four characters (M10, M11, P8, V17) have individual CI's of .5 or less and when these characters are deleted the positions of the clades remain the same (L=114 CI=.728) as in figure 7.10.

Character State Changes

Character state changes are listed in table 7.10 and refer to nodes in figure 7.09. Node 11 consists of *A. boisei*, *A. robustus*, and *A. afarensis* and is defined by a decrease in nuchal crest width, an increase in the porion-zygomaxillare chord, and an increase in glabella projection.

Node 10 is a clade consisting of *A. robustus/ A. afarensis* which is defined by a decrease in palatal depth, a decrease in tympanic-carotid canal chord, an increase in interorbital breadth, and a decrease in upper facial height and cheek height.

Node 13, a clade consisting of *A. africanus*, *H. habilis*, *H. erectus*, and *H. sapiens*, is defined by a decrease in symphyseal height and an increase in nuchal/ occipital area.

Node 12 consists of a clade of *H. habilis*, *H. erectus*, and *H. sapiens*, and the character state changes at this node include a reduction in palate length, a decrease in tympanic-carotid canal chord, an increase in interorbital breadth, and a decrease in upper facial and nasal height.

Node 9 is defined on characters which link *H. erectus* and *H. sapiens*. These include a decrease in mandibular corpus thickness, a reduction of palate proportions, a further decrease in the tympanic-carotid canal, an increase in vault proportions, and a decrease in the height and length of the face.

Deletion of Characters

Five characters have individual CI's of .5 or less (M10, M11, P8, V13, V17) and their deletion results in a shortest tree (L=146 CI=.658) with clades positioned as those in figure 7.09. This is because, of the characters deleted, only two help define a clade (P8 and V17 at Node 9) so their deletion does not affect the construction of the tree.

Part 2

In this section new ancestral states are used from a tree depicting *Gorilla* and *Pan* as sister groups, in a clade which is a sister group to the one containing *H. sapiens* (L=117 CI=.889). The branch and bound option generates 11 trees at 184 steps or less (see Appendix 5), the shortest tree (L=180 CI=.617) having the clades

FIGURE 7.10: SHORTEST TREE: VARIABLE TRAITS:
COMBINED ANCESTOR: A. AFARENSIS AS ROOT

```
                                                            H.S.
                                              *******************1
                                    **********8
                             *******9         ******** 7 H.ER
                             *      *
                    ********10      *** 6 H.HAB
                    *        *
               ****11        ****** 3 A.AFRIC
               *    *
**************12    ******** 5 A.BOIS
*              *
*              ***** 4 A.ROB
*
* 2 A.AFAR
```

L=137 CI=.693

TABLE 7.10: CHARACTER STATE CHANGES: VARIABLE TRAITS

Key:		
	M1 -	Increase in character M1 by one character state
	M1(2)	Increase in character M1 by two character states
	M1	Decrease in character M1 by one character state
	M1(2)	Decrease in character M1 by two character states

NODE 11: A.BOISEI, A.ROBUSTUS, A.AFARENSIS

B19	decrease in nuchal crest width
V20(2)	increase in porion-zygomaxillare chord
F5(3)	increase in glabella projection

NODE 10: A.ROBUSTUS, A.AFARENSIS

P7(2)	decrease in palatal depth at M1
B10	decrease in tympanic-carotid canal chord
F2(2)	increase in interorbital breadth
F12	decrease in upper facial height
F21	decrease in cheek height

NODE 13: A.AFRICANUS, H.HABILIS, H.ERECTUS, H.SAPIENS

M5	decrease in symphyseal height
B19	increase in nuchal crest width
V11(2)	increase in inion chord
V12(4)	increase in inion arc

NODE 12: H.HABILIS, H.ERECTUS, H.SAPIENS

P1	decrease in palate length
B10(2)	decrease in tympanic-carotid canal chord
F2	increase in interorbital breadth
F12	decrease in upper facial height
F13	decrease in nasal height

NODE 9: H.ERECTUS, H.SAPIENS

M7(2)	decrease in corpus thickness
P1(3)	decrease in palate length
P8(2)	decrease in palatal depth at M3
B10	decrease in tympanic-carotid canal chord
V14(2)	increase in nuchal arc
V17(2)	increase in biporionic breadth
V20(2)	decrease in porion-zygomaxillare chord
F12	decrease in upper facial height

positioned as in figure 7.09.

Character State Changes

The character state changes defining each node are identical to those in table 7.10 except that Node 13 does not include B19 as a character state change.

Deletion of Characters

Five characters have individual CI's of .5 or less (M10, M11, P8, V17, F5) and the deletion of these characters results in 2 shortest trees (L=138 CI=.667). The first tree has its clades positioned as in figure 7.09. The second tree only differs in the position of *A. boisei* which, instead of being part of a clade with *A. afarensis* and *A. robustus*, becomes part of a clade which is sister group with them (see figure 7.11). The reason for this is the deletion of F5, one of the traits defining the *A. boisei/ A. robustus/ A. afarensis* clade.

Discussion

Part 1 and 2 show no difference in length, CI, or construction of the tree despite the use of different ancestral states. The deletion of characters in Part 1 and 2 result in trees of shorter length and higher CI, though in part 2 the second tree has a slightly different construction, these sections do share an identical shortest tree. None of the trees generated using variable traits results in CI' s of greater than .700 except when *A. afarensis* is used to root the tree and characters have been deleted. (The CI of .700 is used as an arbitrary 'Rubicon' since non-variable traits (own code) tended to produce trees with CI's less than .700 while those which were recoded tended to produce ones with CI's of greater than .700. Thus the CI's of trees in this section and the next will be assessed in terms of this boundary in order to provide a comparison between the results of each section of this chapter).

7.2.7 Section 4A: All Characters Coded With Different Constants

Part 1

In this section all traits are combined into one data set but each subset is coded using different constants (see tables 7.05 and 7.09 for data). Using the branch and bound option, 13 trees are generated at 365 steps or less (see Appendix 5), with the shortest tree (L=359 CI=.618) in figure 7.12.

Deletion of Hypothetical Ancestor

The deletion of the hypothetical ancestor and the use of *A. afarensis* as the root of the tree, results in two trees (L=300 CI=.690) (see figures 7.13a and b). Figure

FIGURE 7.11: SHORTEST TREE: VARIABLE TRAITS:
NEW ANCESTOR: CHARACTERS DELETED

```
* 1 OUTGROUP
*                                                          H.S.
*                                                 ****************2
*                                        *********9
*                                  *****11        **** 8 H.ER
*                                  *     *
*                           ******12     ** 7 H.HAB
*                           *      *
*                       ***13      ***** 4 A.AFRIC
*                       *   *
***********************14   ******* 6 A.BOIS
                        *
                        *    ********** 3 A.AFAR
                        ****10
                             **** 5 A.ROB
```

L=138 CI=.667

FIGURE 7.12: SHORTEST TREE: ALL TRAITS: COMBINED ANCESTOR:
DIFFERENT CONSTANTS

```
* 1 OUTGROUP
*                                                           H.S.
*                                       *************************2
*                              *********9
*                           **11        ******** 8 H.ER
*                           *  *
*                      ****12  ********* 7 H.HAB
*                      *    *
*                  ***13    *********** 4 A.AFRIC
*                  *   *
*                  *   *      ************** 3 A.AFAR
******************14   ******10
                   *          ************* 6 A.BOIS
                   *
                   ************* 5 A.ROB
```

L=359 CI=.618

FIGURE 7.13A: SHORTEST TREE: ALL TRAITS: COMBINED ANCESTOR:
DIFFERENT CONSTANTS: A. AFARENSIS AS ROOT (TREE 1)

```
                                                            H.S.
                                          ***********************1
                                 *********8
                                 *        ********** 7 H.ER
                         *******10
                         *       *   *************** 4 A.ROB
                ********11       ****9
                *        *           **** 6 H.HAB
***************12        *
*               *        ******* 3 A.AFRIC
*               *
*               ************ 5 A.BOIS
*
*
* 2 A.AFAR
```

L=300 CI=.690

FIGURE 7.13B: SHORTEST TREE: ALL TRAITS: COMBINED ANCESTOR:
DIFFERENT CONSTANTS: A. AFARENSIS AS ROOT (TREE 2)

```
                                                           H.S.
                                          ***********************1
                                **********8
                        *******10         ********* 7 H.ER
                        *       *
                 ******11       ****** 6 H.HAB
                 *      *
****************12      ********* 3 A.AFRIC
*                *
*                *        ************* 4 A.ROB
*                *********9
*                         ******** 5 A.BOIS
*
* 2 A.AFAR
```

L=300 CI=.690

7.13a differs from figure 7.12 in the position of *A. robustus*, which is sister group to *H. habilis*, and *A. afarensis* and *A. boisei* which instead of sister taxa, belong to clades that are sister groups. Figure 7.13b is more similar to figure 7.12 where the positions of *A. robustus* and *A. afarensis* are reversed.

In each of these trees there are a number of characters with a CI of .5 or less. Only those characters common to both are deleted (P5, B2, V2, V9, F17), and this results in a tree (L=261 CI=.720) with clades positioned as in figure 7.13b.

Character State Changes

Character state changes for each node of figure 7.12 are listed in table 7.11. Node 13 includes all hominids except *A. robustus* and is defined by a decrease in external alveolar breadth of the mandible, an increase in palate length, an increase in the length of the base, an increase in vault proportions, a decrease in facial height but an increase in width.

Node 10 is a clade containing *A. afarensis* and *A. boisei* which is defined on the basis of a decrease in mandibular corpus thickness but increase in depth, an increase in depth of the palate, an increase in the length but a decrease in width of the base, an increase in vault proportions, and a decrease in facial length.

Node 12 includes *A. africanus*, *H. habilis*, *H. erectus*, and *H. sapiens* and is defined by a decrease in mandibular breadth, an increase in width of some basal stuctures and an increase in glabella projection (or concavity of nasal bones).

Node 11, containing *H. habilis*, *H. erectus*, and *H. sapiens*, is defined by a decrease in mandibular depth, a decrease in palate breadth, a decrease in bistyomastoid breadth, a decrease in occipital and nuchal chords but an increase in nuchal arc, and a decrease in nasal and orbital height.

Node 9, composed of the sister groups *H. erectus* and *H. sapiens*, is defined by a decrease in mandibular depth, a reduction in palate proportions, a decrease in the width of some basal structures, an increase in vault proportions, and a decrease in nasal height, cheek height, and biorbital breadth.

Deletion of Characters

Seven variable traits (M10, M11, P8, V17, F2, F5, F21) and four non-variable traits (P4, P6, B5, B8) have individual CI's of .5 or less. When they are deleted, the clades of the shortest tree are arranged as in figure 7.12 (L=246 CI=.675). Most of the characters deleted affect Node 9 but their deletion does not affect the configuration

TABLE 7.11: CHARACTER STATE CHANGES: ALL TRAITS:
DIFFERENT CONSTANTS

Key:	
M1 -	Increase in character M1 by one character state
M1(2)	Increase in character M1 by two character states
$\underline{\text{M1}}$	Decrease in character M1 by one character state
$\underline{\text{M1}}$(2)	Decrease in character M1 by two character states

NODE 13: ALL HOMINIDS BUT A.ROBUSTUS

$\underline{\text{M9}}$	decrease in external alveolar breadth
V2	increase in biparietal breadth
F17	increase in bizygomatic tubercle breadth
$\underline{\text{M7}}$	decrease in mandibular corpus breadth
$\underline{\text{P1}}$	decrease in palate length
B13	increase in biforamen ovale line-bitympanic line
B19(2)	increase in nuchal crest width
V11(2)	increase in inion chord
$\underline{\text{F12}}$	decrese in upper facial height

NODE 10: A.BOISEI, A.AFARENSIS

$\underline{\text{B6}}$	decrease in bicarotid canal width
V2	increased biparietal breadth
V8(2)	increased occipital chord
V10(2)	increase in supraglabella-bregma chord
$\underline{\text{M7}}$	decrease in mandibular corpus thickness
M11	increase in mandibular depth at M3
P8	increase in palatal depth at M3
B10	increase in tympanic-carotid canal chord
B13	increase in biforamen ovale line-bitympanic line
V11(3)	increase in inion chord
V12	increase in inion arc
$\underline{\text{V17}}$	decrease in biporionic breadth
V20	decrease in porion-zygomaxillare chord

NODE 12: A.AFRICANUS, H.HABILIS, H.ERECTUS, H.SAPIENS

$\underline{\text{M9}}$	decrease in external alveolar breadth of mandible
B6	increase in bicarotid canal breadth
B8(2)	increase in biforamen ovale breadth
B9(4)	increase in biinfratemporal fossa breadth
F5(4)	increase in glabella projection

NODE 11: H.HABILIS, H.ERECTUS, H.SAPIENS

$\underline{\text{P4}}$	decrease in external alveolar breadth
$\underline{\text{P6}}$	decrease in external arcadal breadth
$\underline{\text{B4}}$	decrease in bistylomastoid breadth
$\underline{\text{V8}}$	decrease in occipital chord
$\underline{\text{F4}}$	decrease in orbit height
$\underline{\text{M11}}$(2)	decrease in mandible depth at M3
$\underline{\text{V13}}$	decrease in nuchal chord
V14	increase in nuchal arc
$\underline{\text{F13}}$	decrease in nasal height

TABLE 7.11: CHARACTER STATE CHANGES: ALL TRAITS:
DIFFERENT CONSTANTS CONTINUED

NODE 9: H.ERECTUS, H.SAPIENS

P2(2)	decrease in internal alveolar breadth
P6(3)	decrease in external arcadal breadth
B2(2)	decrease in foramen magnum width
B4	decrease in bistylomastoid breadth
V1(2)	increased frontal breadth
V2(2)	increased biparietal breadth
V8(2)	decrease in occipital chord
F1	decreased biorbital breadth
M11	decrease in mandible depth at M3
P1	decrease in palate length
P8	decrease in palate depth at M3
V17(2)	increased biporionic breadth
F5	increased glabella projection
F13	decrease in nasal height
F21(3)	decreased cheek height

of the tree.

Part 2

In this section, a new set of ancestral states is used which are obtained from a tree (L=227 CI=.877) where *Pan* and *H. sapiens* are sister groups in a clade which is sister group to the one containing *Gorilla*. Nine trees are found at 374 steps or less (see Appendix 5), with the shortest tree (L=368 CI=.620) having the same arrangement of clades as in figure 7.12.

Character State Changes

The character state changes are identical to those listed in table 7.11 except F17 is not used to define Node 13 and in this node M7 decreases by one extra step.

Deletion of Characters

Four variable traits (M10, P8, F5, F21) and five non-variable traits (P2, P4, P6, B5, B8) are deleted, resulting in a shortest tree (L=271 CI=.664) with clades positioned in a similar manner to those in figure 7.12. The only difference between this tree and the other figures mentioned above is the position of *A. robustus* (see figure 7.14). Again most of the deleted characters affect Node 9. In Node 12 two characters are deleted (F5(4), B8(2)) and their deletion may be what allows *A. robustus* to be included in this clade.

Discussion

Part 1 has a shorter length tree, but the tree in Part 2 has a higher CI, though both are of identical construction. The deletion of characters in Part 1 results in a tree identical to those of 1 and 2 (with no characters deleted), though of shorter length and higher CI. The deletion of characters in Part 2 results in a slightly different tree with the repositioning of *A. robustus.* None of the trees have a CI of greater than .700, even when characters are deleted, except when *A. afarensis* is used as the root of the tree and characters are deleted.

7.2.8 Section 4B: All Characters Coded With The Same Constants

Part 1

In this section, all traits are combined into one data set and each subset is coded using the same constant (see tables 7.07 and 7.09 for data). Using the branch and bound option 9 trees are generated at 318 steps or less (see Appendix 5), with the shortest tree (L=315 CI=.635) in figure 7.15.

FIGURE 7.14: SHORTEST TREE: ALL TRAITS: NEW ANCESTOR:
DIFFERENT CONSTANTS: CHARACTERS DELETED

```
* 1 OUTGROUP
*                                                           H.S.
*                                              ******************1
*                                    **********9
*                                ***11         ****** 8 H.ER
*                                *   *
*                          *****12   ** 7 H.HAB
*                          *     *
*                    *****13     ********** 5 A.ROB
*                    *     *
********************14     ******** 4 A.AFRIC
                     *
                     *   ************ 3 A.AFAR
                     ***10
                         ********* 6 A.BOIS
```

L=271 CI=.664

FIGURE 7.15: SHORTEST TREE: ALL TRAITS: COMBINED ANCESTOR:
SAME CONSTANTS

```
* 1 OUTGROUP
*                                                            H.S.
*                                        ************************2
*                              **********9
*                           **11         ******* 8 H.ER
*                           *  *
*                      ****12  ******* 7 H.HAB
*                      *    *
*                  ***13    ********* 4 A.AFRIC
*                  *   *
*                  *   *     *************** 3 A.AFAR
******************14   *****10
                   *         ************ 6 A.BOIS
                   *
                   ************ 5 A.ROB
```

L=315 CI=.635

Deletion of Hypothetical Ancestor

When *A. afarensis* is made the root of the tree instead of the hypothetical ancestor, a shorter tree (L=258 CI=.717) with higher CI is generated (see figure 7.16). Six characters with low values of CI (.5 or less) are deleted (P5, B2, V2, V9, F4, F17) but the configuration of the tree remains the same (L=216 CI=.759).

Character State Changes

The character states of the nodes of the tree in figure 7.15 are similar to those in Table 7.11 (section 4a). Node 13 does not include M7 but does include an increase in F5. Node 10 does not include P8, B10, B13, or V17; V11 increases by one extra step; and V20 decreases by one extra step. In Node 12, F5 increases by one extra step. Node 11 does not include V13, and M11 decreases by one less step and Node 9 also includes a decrease in M10, an extra decrease in M11 and one less decrease in step of F21.

Deletion of Characters

Ten variable traits (M10, M11, P8, B13, V13, V17 F2, F5, F12, F21) and two non-variable traits (P6, B4) are deleted since their CI's are equal to or less than .5. The shortest tree (L=213 CI=.704) has the same arrangement of clades as that in figure 7.15. At least one character is deleted from each node but the majority are deleted from Node 9.

Part 2

A new set of ancestral states is used in this part of the analysis. The states are obtained from a topology (L=199 CI=.889) where *H. sapiens* and *Pan* are sister taxa, in a clade which was sister group to one containing *Gorilla* (see tables 7.07 and 7.09). This data set generates 9 trees of 323 steps or less (see Appendix 5). The shortest tree (L=319 CI=.636) has the same arrangement of clades as in figure 7.15 (Part 1).

Character State Changes

All the nodes are defined by the same characters as in table 7.11, except for Node 13 in which F17 is not included, but M7 is included in the definition.

Deletion of Characters

Nine variable traits (M10, P8, B13, V13, V17, F2, F5, F12, F21) and three non-variable traits (P2, P6, B2) are deleted as they have CI's of .5 or less. This results in a shortest tree (L=217 CI=.700) with clades positioned as in figure 7.15. Most of the characters deleted affect Node 9, but the three characters deleted from Node 13

FIGURE 7.16: SHORTEST TREE: ALL TRAITS: COMBINED ANCESTOR:
SAME CONSTANTS: A. AFARENSIS AS ROOT

```
                                                            H.S.
                                          ***********************1
                                ********** 8
                                *         ********* 7 H.ER
                        *******10
                        *       *  ************* 4 A.ROB
                 ******11       ***9
                 *      *          **** 6 H.HAB
****************12      *
*                *      ******* 3 A.AFRIC
*                *
*                *********** 5 A.BOIS
*
* 2 A.AFAR
```

L=258 CI=.717

probably account for the movement of *A. robustus.*

Discussion

Part 1 and 2 produce similar trees though the one from part 1 is shorter, the tree from Part 2 has a lower CI. The deletion of characters in Part 1 and 2 produce shorter trees with higher CI's of not much different configuration from that in Part 1. CI's of all trees are less than .700, except when *A. afarensis* is used to root the tree and when characters are deleted.

7.3 Conclusions

7.3.1 Ability To Group Extant Hominids By Sex

Variable traits provide shorter trees with high consistency indices but do not consistently link the sexes. In the majority of trees *Gorilla* males link with *H. sapiens.* Non-variable traits have longer trees but have higher CI's than those of the variable traits. The sexes are consistently linked with one another and *Pan* is closest to *H. sapiens.* The implications of these results are that if variable traits cannot consistently link known, conspecific, sexes, their ability to link likely fossil hominid sister taxa is suspect. That the CI's of variable traits are smaller than those of non-variable traits implies greater homoplasy.

7.3.2 Non-variable traits versus variable traits

When comparing trees with no characters deleted, non-variable trees (either constant) provide shorter trees with higher CI's. When characters are deleted, only one variable tree is shorter than any non-variable tree (figure 7.06 (Section 2A part 2) is one step longer than figure 7.11 (Section 3 part 2)), otherwise non-variable trees are shorter in length with higher CI's.

When *A. afarensis* is used as root, variable traits have a shorter tree but non-variable traits (own code - Section 2A) have a higher CI. Also, the non-variable tree has no characters with an individual CI of .5 or less. When *A. afarensis* is the root, the non-variable tree (recoded) has a shorter tree and higher CI than that using variable traits. Thus overall, non-variable traits generally provide shorter trees with higher CI's.

Variable traits link *A. robustus* with *A. boisei* and *A. afarensis* (even in the longer trees - Appendix 5) while non-variable traits link this species with *H. habilis.* When the two data sets are combined, trees depicting both relationships are produced.

7.3.3 Recoding of Data

When their 'own' constant is used to code the non-variable traits there is a reduction of 70 steps or fewer when characters are deleted, resulting in CI's of greater than .700. When characters were recoded using the larger, variable trait constant, there is only a small change in length due to character deletion because only one character had an individual CI of .5 or less and all shortest trees had a CI of .700 or more.

Using non-variable traits (own constant), the relationship between *A. robustus/H. habilis*, *A. robustus/A. boisei*, or *A. afarensis/A. boisei* is not clear. When using a larger constant *A. boisei* and *A. afarensis* are either sister taxa or sister clades and their relationship to the other hominids is not resolved in the shortest trees. Looking at trees of longer length (see Appendix 5) for both constants, generally *A. robustus/H. habilis* and *A. afarensis/A. boisei* are sister taxa or clades but the affiliations of *A. africanus* are unclear.

The use of a larger constant seems to resolve the situation of *A. robustus/H. habilis* amongst the shortest trees. The use of *A. afarensis* as root provides similar trees in both sections, the only difference being whether *A. afarensis* and *A. boisei* are sister taxa or sister clades.

Overall, the situation seems to be that the use of a small constant (Section 2A) increases between group differences but it results in more homoplasy since the deletion of characters provides much shorter trees. The use of a larger constant (Section 2B) maximising between group similarities, results in less homoplasy, and if parsimony requires minimum homoplasy, then the use of a larger constant may be the better method to use.

The use of a small constant creates a greater difference between character states of different species, resulting in a larger number of character state changes. In other words, for any one trait, two species may have a relatively small difference in original measurement value which, when coded into character states using a small constant, results in, say, two sequential character states, but in identical character states when a larger constant is used. If this occurs for other traits within the sample, then it can cause a greater number of character state changes, and probably numerous cases of reversals, to link sister taxa (or successive sister taxa). The fact that variable traits show greater homoplasy than non-variable traits could be due to this reason as well. Knowing the effect the choice of constant (and range of rai values) has on the amount of homoplasy is important, but to choose the constant just because it produces the least homoplasy, shortest trees, and highest CI's is tautological, and as such is unsound methodology. However, the fact that the analyses are so dependent upon the constant used, hardly supports the notion of them as 'objective'. The use of different constants does determine tree length, CI, and clade composition, and thus these effects should be considered when coding data for cladistic analyses.

The combining of data sets using different constants (Section 4A) results in two trees whether ancestral states or *A. afarensis* are used to root the tree. One of these trees shows *A. robustus* linked with *H. habilis*, and one with *A. robustus* linked with *A. boisei/A. afarensis.* The deletion of characters results in a large decrease in length, but even then the CI does not reach .700. This would seem to indicate that there is a large amount of homoplasy affecting the construction of these trees.

The combination of data sets using the same constants (Section 4B) does not make much difference in terms of the length or CI of the shortest trees. When characters are deleted the length of the trees drops radically and only then do CI's reach .700 or more and most of the characters deleted are variable traits. The effect of using *A. afarensis* as root in both parts of Section 4 results in trees where *A. robustus* and *H. habilis* are sister taxa but in Section 4B there is one tree with *A. robustus* and *A. boisei* as sister taxa.

An examination of the longer trees (Appendix 5) shows *H. sapiens/H. erectus/H. habilis* generally as sister clades, *A. africanus* or *A. robustus* as sister clades or taxa with *H. habilis*, and *A. afarensis* and *A. boisei* as sister clades or taxa. Most of the movement within these trees is performed by *A. africanus* and *A. robustus.*

7.3.4 Final remarks

Overall, the recoded data provide the more parsimonious trees than when non-variable characters are coded using their own constant, and non-variable traits generally perform better than variable traits.

One reason for the performance of the variable traits is that certain characters exhibit more homoplasy than others and if these characters could be eliminated from the analysis this might result in less homoplasy, shorter trees, and higher CI's. One way of determining these characters might be to find and use only variable traits which together consistently link the sexes of the extant hominoids.

In section 1 non-variable traits linked *Pan* and *H. sapiens* and variable traits linked *Gorilla* males and *H. sapiens.* In later sections, non-variable traits linked *A. robustus* and *H. habilis* while variable traits linked *A. robustus*, *A. boisei*, and *A. afarensis.*

An examination of the character state changes allowed an assessment of whether the two situations are connected. *A. robustus* and *A. afarensis* are linked by 3 characters (P7, B10, F12) which also link *Gorilla* males and *H. sapiens*, however, none of the characters which link *H. habilis* and *A. robustus* are ones which link *Pan* and *H. sapiens.* Other authors have noted characters which group together *A. robustus* and specimens usually attributed to *H. habilis* (eg. Chamberlain 1989) but it seems unlikely that these two species shared a close evolutionary relationship. Instead it is probable that these characters evolved in parallel; structural answers to different functional problems.

The importance of this analysis is the differential effect of 1) recoding the data; and 2) using variable or non-variable traits, both of which effect length and CI's of trees but also can significantly effect the relationships between and composition of clades.

To improve the coding method and make it more rigerous would require the standardisation of the method of rejecting outliers, thus making it less subjective. One way of doing this would be to use values within one standard deviation of the mean to represent the "inner" range (see Chapter 4 for a reminder of the method of coding). This would ensure that 68 %, or the majority, of the sample was used as the inner range, and that 16 % of the values below the maximum value as well as 16 % of the values above the minimum value were treated as the outliers. While not a perfect method, it would ensure that each researcher coded his own data, or the same data as other researchers, in exactly the same way.

Obvious criticisms of this analysis are that not enough characters of each type were used, each data set does not equally sample each skull region, and the regions best represented in each data set are different. However, such charges could be levelled against most, if not all, of the cladistic analyses on hominoids available in the literature. The present analyses do indicate that much more care needs to be taken in the choice of characters including an assessment of their variability within the extant hominoids. If fossil hominids, especially the early australopithecines, have high levels of sexual dimorphism, perhaps even higher than the extant hominoids in some instances, then surely the use of variable/ dimorphic traits will have an even greater effect on the resultant trees than is suggested by this analysis.

CHAPTER 8: SUMMARY, FUTURE RECOMMENDATIONS, AND CONCLUSIONS

8.1 Introduction

The fossil record indicates considerable diversity of early hominid forms but there is a lack of consensus on the exact number of species represented. However, the determination of the number of species represented is fundamental to the analysis and interpretation of phyletic and cladistic interrelationships of any larger group, including hominids. In order to facilitate the recognition of distinct species, examination must be made of the amounts of intra- and inter-group variation across the groups under consideration.

An assessment of intra-specific variability should determine whether intra-group diversity reflects individual variation, sexual dimorphism, or heterogeneity of the sample. Some authors, Tattersall (1986) for example, argue that even small morphological differences should be taken to indicate species differences. However, an examination of within-group variation is still necessary to determine species boundaries, otherwise one runs the risk of identifying individuals as separate species on the basis of differences that merely reflect individual variation or sexual dimorphism.

The study of inter-specific variation is also useful for identifying differences and similarities between groups which can then be used to construct measures of relationship, to demonstrate the proximity of two (or more) species. The assessment of both intra- and inter-specific variability, then, is necessary for any project which aims to reconstruct the phylogenies of fossil hominid species.

The purpose of the present research is to use morphological variability in the crania of extant species as a guide to variation to be expected within samples of fossil hominid crania. An attempt was made to find characters of systematic and functional importance applicable to taxonomic and phylogenetic problems in general using univariate, multivariate, and cladistic analyses. Characters were chosen from the available literature in order to represent the different regions of the skull and to reflect the fragmentary nature of the fossil hominid record.

8.2 Meeting the Aims of the Study

The stated aims of this study are:

1) to examine patterns of morphological variation in the crania of extant specis (*H. sapiens*, *Pan*, *Gorilla*, and *Pongo*) to determine if any common pattern of sexual

dimorphism exists which could be used in the assessment of fossil hominid sexual dimorphism;

2) to examine patterns of between-species variability among the crania of extant species to determine if characters exist which could be useful as taxonomic indicators, especially in testing the specific distinctiveness of fossil hominids (ie. to test the homogeneity of fossil species); and

3) to assess the validity of using traits that are variable and/ or dimorphic within species of extant hominoids as taxonomic indicators in systematic analyses of fossil forms.

8.2.1 Results of the Univariate Analysis

Aim 1

The use of univariate techniques identified patterns of within-group variation in the extant hominoids. The analysis showed no common pattern of sexual dimorphism within the modern groups. It uncovered, however, a tendency among the hominoids (fossil and modern) to have dimorphic characters in certain areas. These included the areas of temporal and nuchal muscle attachment, area of kyphosis of the basicranium, width of the palate, mandible, and cranial base, and the extent of facial prognathism - regions which are functionally correlated.

Aim 2

The univariate analysis revealed traits of relatively low variability (CV- coefficient of variation) and low sexual dimorphism which were held in common by all four modern groups. This means that an average taken for any one of these traits should more accurately represent the majority of individuals within each population than traits that are more markedly dimorphic, since the mean value of a trait with a bimodal distribution may represent few, if any, of the individuals within a population. Similarly, the fact that all four modern groups held these traits in common, means that it is likely that the fossil hominids also were of low variability and sexual dimorphism for these traits (by reason of shared ancestry). Even if the traits arose through parallel or convergent evolution, one might expect similar patterns in the fossils since parallel/ convergent evolution results from similar selection pressures which are presumably determining the low values of CV. However, these attributes alone do not make these traits valuable for phyletic or cladistic studies; their usefulness depends primarily upon their ability to discriminate between groups (phyletic valence).

To test whether the non-variable, non-dimorphic traits of this study had high phyletic valence I pooled the data for all four modern groups and for pongids alone and compared the resulting values of CV to those of the fossil groups. Thus these computed vaues of CV represent samples known to be taxonomically diverse. If any of the fossil groups exceeded these values a case could be made for arguing for the heterogeneity of the fossil group, since the fossil sample would be more variable than a sample of four (or three) modern species combined. Thus non-variable, non-dimorphic traits were deemed to be of value because they were held in common by all the modern groups and were useful in testing the homogeneity of groups.

The results of this aspect of the univariate analysis indicated the possible heterogeneity of *H. erectus.* Of the *H. habilis* specimens OH 24 and KNM-ER 1813 may represent specimens of different species. Within the *A. afarensis* sample, A. L. 199.1 and 200.1 may belong to different species, otherwise the degree of sexual dimorphism in *A. afarensis* is, in certain characters, greater than that found in *Gorilla. A. boisei* showed a degree of variability similar to that found in *Gorilla* which is either evidence of sexual dimorphism or heterogeneity. There was not enough evidence to question the homogeneity of the *A. africanus* and *A. robustus* samples. The implications of these results will be discussed below with the results of the multivariate analyses.

As far as I am aware, the method of using computed values of CV to test the homogeneity of species has not previously been used in the analysis of fossil hominids. The use of this method demonstrated that even when taxonomic diversity is known to exist within samples this is not necessarily revealed by values of the CV. Indeed, this method demonstrates that values of CV less than 10 are not always evidence of homogeneity within species.

Both the non-variable, non-dimorphic traits and the remaining characters are useful, but for different purposes. Dimorphic traits are best used to discriminate by sex but only if they are relatively non-variable within each sex. However, the univariate analysis of the present study found no characters of this type which all the modern comparators held in common, that is no common pattern in modern groups of potential sex-discriminating characters. The degree of sexual dimorphism in fossil hominids is still uncertain. If, as seems likely, early hominids were highly sexually dimorphic then it may well be useful to search for characters of low variability within sex but which are highly sexually dimorphic using comparative data from extant species. Otherwise one could assess the fossils by comparing them against each of a selection of extant primate species separately, using this type of character to determine 1) if sexes can be distinguished; and 2) if fossils follow a pattern of sexual dimorphism like that of any one of these modern species.

8.2.2 Results of the Multivariate Analyses

Aims

The multivariate analyses were based on the knowledge of the patterns of variation and dimorphism found within the modern comparators and used both variable and non-variable traits. These patterns were used to 1) determine individual sexes of specimens and/ or to assess the degree of sexual dimorphism within the fossil samples; 2) place limits on the acceptable amount of variation to be found within the fossil samples and thus test their homogeneity.

Principal Components Analysis

The PCA (Principal Components Analysis) used the model of *Gorilla* sexual dimorphism and variability 1) to test the homogeneity of the fossil samples; and 2) as a means of assessing the sex of individual specimens. The analysis identified the sex of some individuals and there was also some indication of heterogeneity within the fossil species. *H. erectus* demonstrated within group differences which may be attributable to regional and/ or temporal differences. Within *A. afarensis*, the variability indicates either a greater degree of sexual dimorphism within this species than in *Gorilla* for some combinations of characters or else that this sample is heterogeneous. KNM-ER 1805 showed some peculiarities of the cranial base which isolate it from other hominoids (see below for a discussion of the implications of these results).

Canonical Variates Analysis

In the CVA (Canonical Variates Analysis), the same fossils were entered as in the PCA except that *H. erectus* was divided into African and Asian specimens and for *A. afarensis*, A. L. 333w.60 and the reconstructed cranium, and LH 4 were entered as two separate groups. The CVA used patterns found in the modern groups to assess homogeneity and the degree of sexual dimorphism of the fossil species. *H. erectus* demonstrated differences in the patterns of sexual dimorphism between African and Asian specimens in the vault. *A. afarensis* showed a different pattern of sexual dimorphism to *Gorilla* in the mandible and palate regions which may be an indication of heterogeneity. In certain combinations of characters *Gorilla* was found to be dimorphic but *A. boisei* was not. Thus while the sex of some individuals was identified these analyses also showed some interesting contrasts in the patterns of the degree of sexual dimorphism between the fossil and modern species.

When patterns of sexual dimorphism are known from samples of modern groups, one might expect to see the same pattern, or at least a tendancy towards the same pattern, within the fossil species. For example, among most mammals males are generally larger than females (McCown 1982) and so within a fossil species one might expect to see either 1) the same pattern; or 2) lack of pattern (no dimorphism); but not the opposite (females larger than males). If a different pattern emerged within the fossil sample then several explanations are possible: 1) the fossil group does not follow the same pattern; 2) the sample size is inadequate; 3) more than one species is being sampled. These explanations may be used to interpret the results of the multivariate analysis of the present study, where *A. afarensis* and *A. boisei* did not follow the primate pattern in certain combinations of characters. Thus knowledge of patterns of sexual dimorphism in modern groups can help to explain patterns of variation within samples of fossil hominids.

8.2.3 Results of the Cladistic Analysis

Aims

If the aim is to discriminate between sexes **within** groups, then non-variable, dimorphic traits (if obtainable) would be the ideal ones to use. If, however, the purpose is to discriminate **between** groups then characters of low within group variability and low sexual dimorphism but high between group variability (ie. with high phyletic valence) would be most useful. Highly variable traits of any type would be of less use in either analysis. This hypothesis was partially tested using cladistic techniques by comparing the results of using non-variable, non-dimorphic characters and variable, dimorphic (at least in *Pongo* and *Gorilla*) characters in separate analyses, and also both types of characters in the same analysis.

Results

The results of the cladistic analysis in the present study indicate differences between non-variable and variable traits with respect to the tree lengths, CI's (Consistency Indices), and clade compositions of the cladograms, with the most parsimonious trees generally being those generated by using the non-variable, non-dimorphic traits. The fact that such differences resulted, indicates that the method is not a totally consistent one, or at least not if traits are chosen indiscriminantly.

The method of coding characters into discrete character states prior to the cladistic analyses was also tested for objectivity. The analyses show the dependence of the results upon the constant used to code the data, and have implications for cladistic analyses of hominoids in general.

The PAUP program allows metric traits to be used in cladistic analyses provided they are appropriately coded into character states. Character state changes, the differences between the character states at any 2 nodes on the cladogram, represent shared derived traits (synapomorphies) which define the monophyletic group but apomorphies (unique derived traits) can also be obtained – traits that can then be used to define any particular species.

If one uses dimorphic traits in the cladistic analysis, traits that have a bimodal distribution, and these are converted into character states (which involves, as part of the process, taking the average value for each trait of each species) it is possible that they may help to determine interrelationships between species. However, these traits are not likely to have any real meaning in biological terms since, as mentioned previously, few, if any, of the individuals within those species will be represented by the average value of any dimorphic trait. If this is true, then surely apomorphies, obtained using the PAUP program (or one like it) are artificial constructs, and as such should not be used to define a species. Instead, species should be defined in terms of relatively invariant/ undimorphic traits if these species definitions are to have any biological reality.

I believe that cladistic methodology can be useful for detailing relationships between fossil groups if: 1) the method used in coding the characters is applied more rigorously and defined in such a way that it can be repeated by other researchers using the same data; 2) the choice of characters is made with an understanding of within group variability; and 3) one understands that the choice of data can have a considerable influence on the observed pattern of between group relationships (O'Higgins 1989b).

8.2.4 Discussion

The Univariate Analysis failed to find a common pattern of sexual dimorphism among the extant hominoids, so that the first aim of this thesis could not wholly be resolved. However, the degree of sexual dimorphism within the fossil hominid species was assessed using the multivariate statistical techniques and thus the thesis' first aim was partly met.

The Univariate Analysis identified characters potentially useful for taxonomic discrimination. These characters were used in the univariate and multivariate analyses as a means of testing the homogeneity of the fossil species. The usefulness of these traits as taxonomic indicators was assessed in the Cladistic Analysis which showed that the above characters (non-variable, non-dimorphic traits) were more successful in grouping the sexes of the same extant species together, and produced more parsimoneous trees, than a set of variable/ dimorphic traits. Thus the second aim of the study has been fulfilled.

The Cladistic Analyses also fulfilled the study's third aim, which was to assess the validity of using variable/ dimorphic traits as taxonomic indicators in systematic analyses.

8.3 Implications of Results

Homo erectus

The difference between the patterns of sexual dimorphism (CVA) as well as the indications of heterogeneity within the *H. erectus* sample (PCA and univariate analysis) can be explained in at least two ways. One explanation involves temporal differences between early and late samples of *H. erectus.* The early African forms of *H. erectus* possess a phylogenetic legacy of primitive traits inherited from an ancestor (cf. Wood 1990). If these traits form a complex of characters affecting the shape and dimensions of the cranium, and this complex becomes more derived over time, then this might result in the kind of differences within the sample of *H. erectus.* Thus the African forms of *H. erectus* are more dimorphic in vault characters than the Asian forms and the latter are more variable in the same characters than the former.

A second explanation of the differences between the samples of *H. erectus* involves the effects of their geographical separation. As discussed above, habitat and resource availability have some effect on the behaviour of an organism and this behaviour can, in turn, affect morphology. If the African and Asian forms of *H. erectus* faced different selection pressures due to differences in habitat, then perhaps it is socioecological contrasts which led to varying expressions of sexual dimorphism between them.

Regardless of which explanation correctly identifies the underlying causes of the differences between African and Asian forms of *H. erectus*, the actual differences probably warrant the inclusion of KNM-ER 3733 and 3883 in a separate species. The results of this study thus support Wood (1990) who would place these specimens (and KNM-ER 730, 820, and 992) in *Homo ergaster*, a separate species from *H. erectus sensu stricto*, on the basis of primitive characters of the cranial vault, mandible, and dentition.

Homo habilis

The question of the homogeneity of *H. habilis* has been the subject of numerous studies, the results of which indicate that it should be sub-divided into different species, but as yet no consensus has been reached as to how this division should be made (eg. Groves and Mazak 1975; Wood 1978; Howell 1978a; Dean and Wood 1982b; Stringer 1986; Chamberlain 1987, 1989; Chamberlain and Wood 1987; Leakey *et al.* 1989).

The results of the Univariate Analysis of this study only partially help to resolve this problem in that they indicate that at least OH 24 and KNM-ER 1813 are unlikely to belong to the same species. The Multivariate Analysis of the Base, Face, and Regional Combination also showed that KNM-ER 1470 shared affinities with African *H. erectus*. This collection of fossil hominids shows greater variability compared to the extant species but this may be evidence of 1) a species in transition; 2) mosaic evolution; or 3) more than one species. Thus further research, and probably larger samples, are needed to resolve this problem.

KNM-ER 1805 is presumed to be a male on the basis of the size of its braincase and palate. However, its mandible is smaller than one would expect for a male. Also, this specimen has been isolated, in the multivariate analysis of this study, as having unique basicranial proportions. The aspect of the basicranium which makes KNM-ER 1805 unique is the position of its foramina ovale which are situated more anteriorly than in other hominids.

The function of the foramina ovale are to transmit the third division of the trigeminal (5th) cranial nerve from the brain to the face, nose, palate, mouth, and mandible. This nerve has both sensory and motor functions. It conveys the sensations for touch, pain, and temperature from parts of the face, nose, palate, teeth, and tongue to the brain. Injury to this part of the nerve results in loss of sensation of touch, temperature, and taste. At the same time it is the nerve of the muscles of mastication and, if injured, results in impaired action of the mandible from paralysis of the muscles of mastication (Johnston and Whillis 1956; Tortora and Anagnostakos 1987). Thus damage to the trigeminal nerve may provide some explanation for KNM-ER 1805's peculiar morphology.

If the trigeminal nerve was damaged in KNM-ER 1805 while it was young, this might have resulted in the abnormal growth of the mandible. However, more research needs to be done to ascertain if this hypothesis is a realistic one.

The fact that KNM-ER 1805 lived to adulthood means that this condition did not affect its life expectancy and also that the individual could have contributed to the reproduction of offspring. However, its unique morphology makes the taxonomic placement of the specimen difficult. There is increasing evidence that *H. habilis* or 'early *Homo*' consists of two or more species (eg. Stringer 1986; Chamberlain 1987).

Thus while KNM-ER 1805 provides an interesting example of palaeopathology, it would be unwise to use it as the holotype of any new species.

A. boisei

In some characters *A. boisei* and *Gorilla* showed differences in the degree of sexual dimorphism they exhibited. This is probably due to the ecological conditions in which these two species evolved which would have led to differences in social groupings and behaviour, which in turn would contribute to differing degrees of sexual dimorphism in at least some characters. Foley (1989), for example, proposes a social organisation for the robust australopithecines where subgroups developed containing females attached to a single male as in *Gorilla*, but with these subgroups operating within the context of a larger group. This kind of social organisation would have been most appropriate in an open habitat due to the pressures of predation. The fact that such differences in the degree of sexual dimorphism exist between *Gorilla* and *A. boisei*, and that they inhabited different environments, means that *Gorilla* may not be the most appropriate model to illuminate intra-group variability within *A. boisei*. Instead, it might be useful to use one of the savannah baboons as a comparator, since their habitats, and the underlying functional causes of sexual dimorphism in these species (or sub-species), would be more similar to those of *A. boisei*.

A. afarensis

The results of the multivariate analyses indicated that the sample of *A. afarensis* may be heterogeneous. One would expect such a primitive hominid such as *A. afarensis* to show signs of its antecedents and since Sibley and Alquist (1984) claim that *Pan* shares a common ancestor with the hominid lineage it is to this modern species one should turn to for comparison. Indeed, Kimbel *et al.* (1985) demonstrate similarities in cranial features between *Pan* and *A. afarensis*. Also, Stern and Susman (1983) infer a degree of arboreal behaviour from the postcranial bones of *A. afarensis*. If *Pan* is the closest non-human primate relative of *A. afarensis* and if the common ancestor of both species was arboreal, then it is reasonable that some legacy of this form of locomotion be found in *A. afarensis*. However, one would not expect a marked degree of sexual dimorphism within this species, since arboreal species tend not to be very dimorphic, unless *A. afarensis* is considerably derived from its ancestors. Similarly, one would not expect to find morphological differences between sexes to the degree described by Senut and Tardieu (1985). Finally one should note the suggestion by Tuttle (in Stern and Susman 1983:309) that Lucy (A. L. 288.1) could not have made the Laetoli footprints. Instead it would be more reasonable to infer that two or more species were present at this time.

The first major deviation in adaptive strategy of hominids from the ancestral pre-hominid is assumed to be bipedalism. This, along with the knowledge that evolution occurs in a mosaic fashion, allows one to expect some conservatism in cranial features, but variability, even diversity, in postcranial anatomy. Thus if two or more species of *A. afarensis*-like hominids existed, then it may be easier to divide them on the basis of postcranial anatomy where the specimens showing arboreal traits form one species and the more terrestrial ones, another. However, the problem then remains the fundamental one of how to associate postcrania with crania.

Conservatism in cranial traits would make it difficult to divide the *A. afarensis* cranial material by species. However, there is some indication of heterogeneity in this sample as shown in the Univariate and Multivariate Analyses of this study. I would tentatively suggest that within the Hadar sample, at least A. L. 333w.60 and perhaps A. L. 207.13 may belong to a different species from the remaining specimens. A. L. 199.1 and 200.1 may not belong to the same species and, while the former could be affiliated with the remaining *A. afarensis* specimens, A. L. 200.1 may well belong in the same group as A. L. 333w.60. This is not an unreasonable suggestion, since this palate and mandible were judged to be sufficiently similar to form part of the reconstructed cranium (Kimbel *et al.* 1984). Also, LH4 shows considerable size differences in its dentition when compared to the reconstructed *A. afarensis* mandible, and so it might even belong to a third group of hominids (either species or subspecies). That the *A. afarensis* sample consists of two or more species and that there was a radiation of early hominid forms, seems to be the most parsimonious reasoning based on the results of the present study.

8.4 Future Recommendations

As the analysis of my data progressed, the utility of non-variable, non-dimorphic traits as taxonomic indicators became more apparent. However, I believe that further tests need to be made to corroborate the findings of the present analysis. These could include any or all of the following:

1. an increase in the number of non-variable, non-dimorphic traits studied, including data from post-cranial elements;
2. test the existence/ utility of the above two types of traits using other primate groups;
3. include data from Miocene hominoids in the outgroup of the cladistic analyses

in order to obtain an alternative assessment of the ancestral hominid morphotype.

Once these tests are carried out and assessed it would then be useful to expand the fossil hominid data base to include specimens of archaic *H. sapiens*, Neanderthals, and other Middle/ Upper Pleistocene groups which, according to Tattersall (1986), probably consist of a number of different species.

8.5 Conclusions

The results of my study indicate that hominoid species differ in the degree of sexual dimorphism they exhibit and that the pattern of within-species variability for each species may be unique. This is not to say that there will not be some overlap in the number and kind of sexually dimorphic traits that can be held in common between any two species, just that two species are not likely to have identical patterns of sexual dimorphism. Applying this reasoning to fossil hominid species, one is faced with the fact that the pattern of fossil sexual dimorphism is unknown, and perhaps unknowable. Fossil species are, in the last resort, plausible models that are consistent with available data and new evidence may prompt reassessment of even living, established, species. Fossil species, especially when based on incomplete specimens comprising limited samples, are particularly fragile constructs. However, knowledge of modern intra-specific variation, may enable one to place limits on the degree of sexual dimorphism one would accept before suspecting that a sample was heterogeneous, but we cannot expect to match the pattern of sexual dimorphism of any one species *exactly* with that of any other species, living or fossil. The univariate analysis of the present study, for example, found that although there was no common **pattern** of sexual dimorphism held in common by all four modern groups, there were certain regions of the skull which **tended** to contain sexually dimorphic characters – a fact supported by other studies (eg. Leutenegger 1982, McCown 1982).

In the past relatively little attention has been paid to the intra-specific variability of morphological characters. Also, few attempts have been made to discriminate between types of characters and to put characters to different uses. Recently workers have begun to appreciate the implications of intra-specific variability and have examined various fossil samples in this light. Kimbel and White (1988), for example, use the coefficient of variation (CV) as a measure of homogeneity within samples of fossil hominids using measurements from the canine and post-canine teeth. They maintain that the breadth of M1 and M2 are generally the least variable amongst the extant primate species. They found that for the maxillary M2, *A. africanus* had a CV of 8.2

and also a bimodal distribution of values which led them to suspect a heterogeneous sample of *A. africanus*. These authors can be criticised for their use of this evidence on a number of counts:

1) they do not demonstrate that this trait has phyletic valence (ie. can distinguish between groups);

2) they do not establish whether or not M2 breadth is sexually dimorphic in extant hominoids;

3) they do not discuss the fact that *Pan troglodytes* has a CV of 9.1;

4) they do not show the distribution of values for the maxillary M1 breadth dimensions of *A. afarensis*.

Thus, although the homogeneity of *A. africanus* may be suspect on the grounds of other evidence presented by these authors, the evidence of *A. africanus* M2 dimensions cannot be said to substantiate a claim for heterogeneity of the species sample. I believe that future researchers must take more care in their choice of characters and in their assessment of their variability if useful conclusions are to be reached from phyletic or cladistic analyses.

The present study involved an analysis of intra- and inter-specific variability among Plio-Pleistocene hominids based on models derived from modern *H. sapiens* and pongids. Metrical cranial characters were surveyed in order to assess the functional and phyletic implications of their variability within the available early hominid sample using statistical and cladistic analytical techniques. The study has demonstrated that characters have different properties related to the degree to which they vary or are dimorphic within species and that using these characters for different purposes has the potential to enhance future phyletic and cladistic studies.

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Appendix 1:
Catalogue Numbers and Locations of Extant Primate and Human Specimens

Catalogue No.	Sex	Location	Catalogue No.	Sex	Location
Pan troglodytes			*Gorilla gorilla*		
1939.3369	M	BMNH	1939.912	M	BMNH
1924.8.6.1	M	BMNH	36.7.14.1	M	BMNH
1939.965	M	BMNH	1939.929	M	BMNH
1939.3363	M	BMNH	23.11.29.6	M	BMNH
1939.3364	M	BMNH	1948.5.4.1	M	BMNH
1939.3362	M	BMNH	25.1.4.1	M	BMNH
87.12.1.2	M	BMNH	1939.913	M	BMNH
1939.3377	M	BMNH	1939.915	M	BMNH
1939.3385	M	BMNH	48.435	M	BMNH
1939.3365	M	BMNH	1939.9.2.4	M	BMNH
1864.12.1.7	F	BMNH	1939.926	F	BMNH
1939.957	F	BMNH	1939.927	F	BMNH
20.4.13.2	F	BMNH	1939.933	F	BMNH
367.7.2	F	BMNH	1939.914	F	BMNH
1939.3383	F	BMNH	1857.11.2.3	F	BMNH
27.1.4.1	F	BMNH	1948.3.31.2	F	BMNH
1939.3367	F	BMNH	86.758	F	BMNH
1968.7.5.11	F	BMNH	23.11.29.8	F	BMNH
1939.3379	F	BMNH	1939.922	F	BMNH
1939.3366	F	BMNH	1939.934	F	BMNH
Pongo pygmaeus			*Homo sapiens*		
1948.7.6.3	M	BMNH	PC73E825	M	BMNH
1976.1431	M	BMNH	PC76E953	M	BMNH
1844.3.30.18	M	BMNH	PC73E839	M	BMNH
1856.11.8.2	M	BMNH	PC73E816	M	BMNH
1976.1435	M	BMNH	PC76E1037	M	BMNH
92.11.5.3	M	BMNH	PC76E1025	M	BMNH
1976.1426	M	BMNH	PC69B98	M	BMNH
1976.1440	M	BMNH	PC69B94	M	BMNH
1976.1428	M	BMNH	PC71B207	M	BMNH
18.5.23.1	M	BMNH	PC70B143	M	BMNH
1976.1427	F	BMNH	PC73E832	F	BMNH
1976.1415	F	BMNH	PC76E952	F	BMNH
1976.1430	F	BMNH	PC75E796	F	BMNH
1976.1418	F	BMNH	PC73E819	F	BMNH
1976.1422	F	BMNH	PC75E794	F	BMNH
1879.11.21.214	F	BMNH	PC76E197	F	BMNH
1986.1119	F	BMNH	PC69B100	F	BMNH
1948.7.6.1	F	BMNH	PC72C566	F	BMNH
1986.1100	F	BMNH	PC72C568	F	BMNH
1986.1113	F	BMNH	PC72D574	F	BMNH

APPENDIX 2:

Definitions of Craniometric Points

ABB	The point of maximum breadth on the external surface of the maxillary alveolar border, wherever found.
ABL	The point of maximum breadth on the internal surface of the maxillary alveolar border, wherever found.
AE	The lowest point on the articular eminence.
AL	The most inferior point on the alveolar septum between the upper central incisors.
AM	The most lateral point on the alveolar margin on the external surface, below ZR.
AST	The point where the temporal, parietal and occipital sutures meet.
AU	Located outside of the root of the zygomatic process at the deepest incurvature near the auditory meatus.
B	The point of maximum breadth on the buccal surface of a tooth in the maxilla, wherever found.
BE	A point on the alveolar margin posterior to the lower third molar on the external surface.
BI	A point on the alveolar margin posterior to the lower third molar on the internal surface.
BA	The anterior edge of the foramen magnum in the midline.
BP	Point on the parietal above the supramastoid crest wherever maximum biparietal breadth is found.
BR	Located on the superior surface of the skull where the frontal sutures and sagittal suture meet.
C	The midpoint of the internal alveolar margin of the upper canine.
CB	A point on the base of the mandible, perpendicular to CH.
CC	Center of the carotid canal at the point of intersection of the maximum anteriopósterior and mediolateral diameters.
CH	The most anterior point of the mandible.
CR	A point on the internal surface of the mandibular corpus at the point of its maximum thickness, at, or posterior to, the upper third molar.

CR1	A point on the external surface of the mandibular corpus at the point of its maximum thickness, at, or posterior to, the upper third molar.
CRH	The most superior point on the coronid process.
DA	The intersection of the frontomaxillary suture with the lacrimal suture at the apex of the lacrimal fossa.
F	Point on the frontal bone perpendicular to the median plane wherever maximum breadth is found.
FH	(Frankfurt Horizontal) The line passing through the lowest point on the lower margin of the orbits and porion.
FM	Border of the foramen magnum at the point of maximum width.
FMA	(frontomalare anterior) The most anterior point on the frontomalar suture.
FMT	(frontomalare temporal) The most posterior point on the frontomalar suture.
FO	Center of the foramen ovale at the point of intersection of the maximum anteroposterior and mediolateral dimension.
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 symphasis in the midline.
GO	(gonion) The most lateral external point of the junction of the mandibular body and the ascending ramus.
I	The midpoint of a line joining the tips of the upper central incisors.
ID	A point on the alveolar margin posterior to the upper central incisor.
IN	(inion) A point on the inferior nuchal line in the midline.
INF	(infradentale) The most superior point on the alveolar septum between the lower central incisors.
IP	A point on the palate posterior to the central incisors, in the midline.
LA	(lambda) Where the sagittal suture and temporal sutures meet at the intersection of the occipital and parietal bones in the midline.
LM	A point on the external surface of the alveolar margin at the lower first molar.

LMI	A point on the inferior surface of the mandibular corpus below the lower first molar.
LM3	A point on the external surface of the alveolar margin at the lower third molar.
LM3I	A point on the inferior surface of the mandibular corpus below the lower third molar.
M	The tip of the mastoid as seen from the underside.
MC	The most posterior point on the mandibular condyle.
MF	The deepest point of the lateral edge of the mandibular fossa.
MF1	The deepest point of the mandibular fossa.
ML	Tip of the mastoid as seen from the side.
MM	The lower margin of the maxilla mesial to the masseter attachment at its greatest concavity.
MN	The most lateral point on the edge of the nasal aperture.
MT	The most posterior point on the maxillary tuberocity.
MW	The anterior edge of the mastoid at its greatest width.
MW1	The posterior edge of the mastoid at its greatest width.
M1	The rear of the lateral side of the mastoid.
M1D	A point on the alveolar margin mesial to the upper first molar.
M1P	A point on the palate mesial to the upper first molar, in the midline.
M3	The most posterior point on M3.
M3D	A point on the internal alveolar margin next to the upper third molar.
M3P	A point on the palate mesial to the upper third molar.
N	(nariale) The lowest point on the nasal aperture on either side in the midline.
NA	(nasion) The intersection of the frontonasal suture and the midline.
NB	The point on the nasal bone at the point of minimum transverse breadth.
O	The most lateral point on the orbital edge.

O1	The most superior point on the orbital edge.
O2	The most inferior point on the orbital edge.
O3	The point on the inferior orbital rim which is the least distance from MM.
OP	(opisthion) The posterior edge of the border of the foramen magnum in the midline.
OPC	(opithstho-cranion) The point on the occipital which is the most posterior point in the median sagittal plane.
OR	(orale) A line joining the posterior alveolar borders of the upper incisors.
PA	The most anterior point on the inferior surface of the petrous temporal bone.
PG	The most inferior point of the postglenoid process.
PO	(porion) The uppermost point in the margin of the external auditory meatus.
PR	(prosthion) The most anteriorly prominent point, in the midline, on the alveolar border, above the septum between the upper central incisors.
RB	The point on the anterior border of the ascending ramus wherever the minimum ramus breadth is found.
RB1	The point on the posterior border of the ascending ramus wherever the minimum ramus breadth is found.
SB	The estimated position of the sphenooccipital synchrondosis in the midline.
SC	The most lateral on the parietal above the supramastoid crest.
SCR	A point to the right of the sagittal crest on the cranial vault perpendicular to FH.
SCL	A point to the left of the sagittal crest on the cranial vault perpendicular to FH.
SCT	A point on the top of the sagittal crest on the cranial vault perpendicular to FH.
SG	(supra-glabellare) The point at which the convex profile of the frontal bone changes to meet glabellare.
SM	The estimated centre of the stylomastoid foramen.
SP	The midpoint of the posterior aspect of the base of the styloid process or centre of the styloid pit if the process is missing.

SS	(subspinale) The deepest point seen in the profile of the nasoalveolar clivis (*H. sapiens*), or the intersection of the plane of the margins of the piriform aperture with the nasoalveolar clivis, in the midline.
TM	The point on the uppermost part of the temporal muscle mark above PO perpendicular to FH.
TP	The most inferior point on the lateral end of the tympanic plate.
Z	The estimated centre of the foramen mentalia.
ZA	A point superior to ZS on the lateral surface of the zygomatic process of the temporal where the maximum thickness is found.
ZA1	A point superior to ZS on the medial surface of the zygomatic process of the temporal where the maximum thickness is found.
ZM	(zygomaxillare) The intersection of the zygomaxillary suture and the masseter muscle attachment on the inferior surface.
ZO	(zygoorbitale) The intersection of the orbital margin and the zygomaxillary suture.
ZR	(zygomatic root) The point at which the convex profile of the zygomatic changes to meet the alveolar bone.
ZS	(zygotemporal suture) The most inferior edge of the zygotemporal suture.
ZS1	The point perpendicular to ZS on the superior surface of the zygomatic process of the temporal, wherever found.
ZT	(zygomatic tubercle) The point of attachment of the furthest extention of the masseter muscle. Sometimes the same as ZM.
ZY	(zygion) The most lateral point on the zygomatic.
ZYO	The most lateral point on the zygomatic at the plane of the orbits.

APPENDIX 2: Continued

Definitions of Measurements

M1	Bigonial breadth.	GO-GO
M2	Foramen mentalia breadth.	Z-Z
M3	Maximum length of the mandible.	MC-CH
M4	Minimum ramus breadth.	RB-RB1
M5	Symphyseal height	INF-GN
M6	Coronoid height.	CRH-CB
M7	Maximum thickness of the mandibular corpus.	CR-CR1
M8	Maximum internal breadth from alveolar margins of the mandible.	BI-BI
M9	Maximum external breadth from alveolar margins of the mandible.	BE-BE
M10	Mandibular depth at M1.	LM-LMI
M11	Mandibular depth at M3.	LM3-LM3I
M12	Mandibular arcadal length.	INF-M3/M3
P1	Palate length.	OR-ST
P2	Maximum lingual breadth between alveolar margins.	ABL-ABL
P3	Maxillo-alveolar length.	PR-MT/MT
P4	Maximum external breadth between outer margins.	ABB-ABB
P5	Arcadal length.	I-M3/M3
P6	Maximum arcadal breadth.	B-B
P7	Palatal depth at M1.	M1P [M1D/M1D
P8	Palatal depth at M3.	M3P [M3D/M3D
P9	Bicanine breadth.	C-C
B1	Foramen magnum length.	BA-OP
B2	Foramen magnum width.	FM-FM
B3	Bitympanic width.	TP-TP
B4	Bistylomastoid width.	SM-SM
B5	Bistyloid width.	SP-SP
B6	Bicarotid canal width.	CC-CC
B7	Bipetrous width from apex to apex of the petrous temporal bones.	PA-PA
B8	Biforamen ovale width (centre).	FO-FO
B9	Biinfratemporal fossa width.	IT-IT
B10	Length of the tympanic plate from the lateral end of the tympanic to the centre of the carotid canal.	TP-CC
B11	Length along the petrous temporal bone from the centre of the carotid canal to apex.	CC-PA
B12	Distance between biinfratemporal line and bitympanic line.	IT/IT-TP/TP
B13	Distance between biforamen ovale line and bitympanic line.	FO/FO-TP/TP
B14	Distance between biinfratemporal line and basion.	IT/IT-BA
B15	Basioccipital length.	SB-BA
B16	Biasterionic breadth.	AST-AST
B17	Maximum breadth across supramastoid crests.	SC-SC
B18	Bimastoid breadth.	M-M
B19	Nuchal crest width.	OP-M1
B20	Lateral nuchal crest arc.	IN (M1
B21	Sphenooccipital synchrondosis-staphlyon chord.	SB-ST

B22	Staphlyon-basion chord	ST-BA
B23	Articular eminence height.	MF [AE
B24	Post-glenoid process height.	MF1 [PG
V1	Maximum frontal breadth.	F-F
V2	Maximum biparietal breadth.	BP-BP
V3	Frontal arc.	NA^BR
V4	Frontal chord.	NA-BR
V5	Parietal arc.	BR^LA
V6	Parietal chord.	BR-LA
V7	Occipital arc.	LA^OP
V8	Occipital chord.	LA-OP
V9	Basi-bregmatic height.	BA-BR
V10	Supraglabellar-bregmatic chord	SG-BR
V11	Inion chord	LA-IN
V12	Inion arc	LA^IN
V13	Nuchal chord.	IN-OP
V14	Nuchal arc.	IN^OP
V15	Height of temporal muscle mark.	PO-TM
V16	Temporal muscle mark arc.	FMT (PO
V17	Biporionic breadth.	PO-PO
V18	Porion-dacryon chord	PO-DA
V19	Porion-zygoorbitale chord	PO-ZO
V20	Porion-zygomaxillare chord	PO-ZM
V21	Naso-occipital length.	NA-OPC
V22	Biauricular breadth.	AU-AU
V23	Mastoid length.	FH-ML
V24	Mastoid width.	MW-MW1
F1	Maximum biorbital breadth.	O-O
F2	Interorbital breadth.	DA-DA
F3	Maximum orbital breadth.	DA-O
F4	Maximum orbital height.	O1-O2
F5	Glabella projection.	G [S/SG
F6	Bizygomatic breadth at the plane of the orbits.	BZO-BZO
F7	Maximum bizygomatic breadth.	BZ-BZ
F8	Upper facial breadth.	FMA-FMA
F9	Bimaxillary chord.	ZM-ZM
F10	Zygomaxillary subtence.	SS [ZM/ZM
F11	Subspinale-zygomaxillare chord.	SS-ZM
F12	Upper facial height.	NA-PR
F13	Nasal Height.	NA-N
F14	Maximum nasal breadth.	MN-MN
F15	Simotic chord.	NB-NB
F16	Distance from the root of the zygomatic to the alveolar margin.	ZR-AM
F17	Bizygomatic tubercle breadth.	ZT-ZT
F18	Superior malar length.	FMA-ZS
F19	Maximum malar length.	ZO-ZS
F20	Inferior malar length.	ZM-ZS
F21	Minimum cheek height.	MM-O3
F22	Superior facial length.	BA-PR
F23	Lateral facial length.	FMA-PO
F24	Basi-nasal length.	BA-NA
F25	Basi-alveolar length.	BA-AL
F26	Zygomatic arch depth.	ZS-ZS1
F27	Zygomatic arch thickness.	ZA-ZA1

KEY TO APPENDIX 2 NOTATION

AA-BB	Length of chord from AA to BB.
AA^BB	Length of arc from AA to BB.
AA/BB	Length of line from AA to BB.
AA (BB	Arc from AA to BB.
AA [BB/CC	Distance subtended by AA from line BB/CC.

APPENDIX 3: DATA OF MODERN HUMANS, PRIMATES, AND FOSSIL HOMINIDS

HOMO SAPIENS

CAT	M1	M2	M3	M4	M5	M6	M7	M8
73E832	9.02	4.12	10.30	2.92	2.35	5.55	1.60	4.76
76E952	8.75	4.36	9.30	3.18	2.63	5.20	1.50	5.07
75E796	8.01	4.27	9.95	2.60	2.91	5.61	1.41	4.64
73E819	8.18	4.18	10.00	3.24	3.15	6.10	1.40	5.15
75E794	9.75	4.40	9.90	3.45	2.62	[6.00]	1.50	[5.78]
73E825	9.77	4.56	9.50	3.48	3.24	6.45	1.40	4.60
76E953	10.70	4.79	10.10	3.06	2.83	6.10	1.46	[5.40]
73E839	.	.	[10.60]	3.19	.	.	1.34	.
73E816	11.14	5.09	[10.80]	3.74	3.52	[7.00]	1.70	6.07
76E1037	10.93	4.50	10.40	3.41	[3.20]	7.20	1.58	5.00
76E1025	9.44	4.55	9.90	3.12	3.54	7.41	1.57	5.50
70C197	9.75	4.53	[10.10]	3.38	2.66	7.12	1.40	5.45
69B100	9.48	4.13	[9.40]	3.04	2.50	5.50	1.53	5.50
69B098	11.13	4.50	10.20	3.70	2.80	7.24	1.80	6.30
69B094	10.90	4.43	10.40	3.83	3.70	7.22	1.80	5.84
71B207	[10.40]	[5.00]	[11.40]	3.28	3.80	.	1.82	5.76
70B143	12.60	4.63	10.80	3.50	3.35	6.12	1.70	6.50
72C566	8.65	4.62	9.50	3.25	2.50	6.43	1.20	[5.54]
72C568	.	4.30	.	.	2.75	.	1.70	4.57
72D574	9.90	4.25	9.50	3.00	3.00	5.88	1.40	5.70

CAT	M9	M10	M11	M12	P1	P2	P3	P4
73E832	6.45	2.15	.	[3.40]	4.40	[4.00]	5.30	[5.68]
76E952	6.80	2.41	2.41	4.30	4.28	3.51	4.94	5.60
75E796	6.45	2.51	2.34	4.42	3.86	3.92	4.91	5.90
73E819	6.26	2.80	2.45	4.17	4.21	3.10	.	5.54
75E794	7.09	2.60	2.40	5.10	4.46	[3.77]	5.20	5.78
73E825	6.35	2.91	2.87	3.40	4.18	4.12	4.95	6.17
76E953	[6.80]	3.18	2.88	4.20	.	.	.	.
73E839	.	3.12	3.05	.	4.30	4.33	.	6.14
73E816	7.51	3.00	3.13	[4.70]	5.00	4.77	5.84	.
76E1037	6.85	2.94	2.69	[3.42]	4.44	4.30	5.14	.
76E1025	7.01	3.59	3.22	5.07	5.12	4.63	6.12	7.10
70C197	[7.00]	2.35	2.00	[3.82]	4.62	3.97	5.30	6.01
69B100	6.65	2.30	2.45	4.30	4.30	4.18	5.17	6.24
69B098	7.55	2.65	2.40	4.60	4.44	3.80	5.29	6.70
69B094	7.24	3.25	2.80	5.08	4.80	4.42	5.70	6.50
71B207	7.00	3.20	3.10	4.70	5.10	.	6.35	.
70B143	7.60	2.80	2.70	4.80	4.83	4.10	5.40	6.44
72C566	[6.87]	2.55	2.50	[4.00]	3.75	4.12	4.65	6.22
72C568	6.20	2.50	2.55	4.14	4.48	[3.95]	5.13	6.20
72D574	6.80	2.70	2.40	4.50	4.50	4.24	5.30	6.05

HOMO SAPIENS

CAT	P5	P6	P7	P8	P9	B1	B2	B3
73E832	.	.	.98	.	2.40	.	[3.20]	10.87
76E952	5.15	5.79	1.24	1.19	2.28	3.42	2.74	9.76
75E796	5.01	6.00	1.22	1.29	2.30	3.20	2.77	9.40
73E819	.	.	1.60	.	2.09	3.46	2.54	8.83
75E794	4.80	6.02	1.20	1.08	2.26	3.98	3.07	10.94
73E825	4.85	6.19	1.07	1.32	2.48	3.10	3.06	10.30
76E953	.	.	.	[1.00]	2.17	3.47	3.38	10.48
73E839	4.76	6.34	.75	1.18	2.50	4.37	[3.14]	11.07
73E816	.	.	1.39	1.36	2.97	3.70	3.11	10.94
76E1037	4.18	.	.91	1.49	2.53	3.75	3.15	11.05
76E1025	5.17	7.07	1.32	1.70	2.68	3.63	[3.00]	10.62
70C197	.	.	[1.20]	[1.10]	2.35	3.22	[3.20]	10.18
69B100	4.94	6.34	.82	.78	2.55	3.15	2.68	10.00
69B098	5.14	[6.60]	1.45	1.50	2.58	3.00	2.80	11.80
69B094	5.20	6.70	1.25	.95	2.45	3.32	2.85	10.85
71B207	.	.	1.80	.	2.70	3.55	2.77	10.45
70B143	5.04	.	1.50	1.40	2.60	3.65	2.84	9.70
72C566	4.38	[6.00]	1.20	1.40	2.16	.	.	10.30
72C568	5.32	6.15	.85	.90	2.49	[3.75]	3.22	[10.12]
72D574	5.05	6.27	1.00	1.05	2.20	2.91	2.76	9.52

CAT	B4	B5	B6	B7	B8	B9	B10	B11
73E832	9.19	8.58	6.65	[3.00]	5.40	[7.60]	2.30	[2.00]
76E952	7.83	7.46	5.80	3.37	5.04	6.50	2.25	1.74
75E796	7.49	6.68	5.11	2.91	4.56	6.54	2.78	1.93
73E819	7.29	6.95	4.87	[3.27]	4.63	6.81	2.14	1.75
75E794	8.74	8.60	6.30	3.66	5.40	6.74	2.77	1.79
73E825	8.40	8.15	6.00	3.65	[4.70]	6.90	2.28	2.18
76E953	8.73	8.45	5.83	3.80	4.90	6.30	2.84	1.26
73E839	9.18	8.93	6.64	[3.50]	5.36	6.92	2.62	2.45
73E816	9.13	8.70	6.41	4.24	5.53	6.81	2.58	1.82
76E1037	9.60	8.95	6.46	3.85	5.37	6.50	2.52	1.74
76E1025	9.12	8.50	6.60	[3.68]	[5.74]	6.60	2.59	2.10
70C197	8.80	7.82	6.10	3.30	5.40	7.95	2.50	2.05
69B100	8.10	7.60	5.70	[3.10]	4.70	6.20	2.34	2.00
69B098	9.30	8.60	7.04	[3.25]	5.33	7.70	3.10	[2.05]
69B094	8.55	7.50	5.70	3.30	5.45	6.60	2.80	1.90
71B207	8.90	8.28	5.95	3.54	5.35	7.10	2.60	1.97
70B143	8.17	7.85	5.40	3.25	4.68	7.24	2.58	2.20
72C566	8.40	[8.10]	5.93	3.14	5.15	6.53	2.36	1.90
72C568	8.44	8.00	6.00	[2.70]	4.80	6.90	2.64	[1.94]
72D574	8.26	7.54	5.70	3.90	4.60	6.10	2.10	1.47

HOMO SAPIENS

CAT	B12	B13	B14	B15	B16	B17	B18	B19
73E832	4.80	2.80	.	.	12.74	13.22	11.10	6.38
76E952	4.90	2.40	4.50	2.35	10.84	11.30	[9.50]	5.40
75E796	4.90	3.30	3.70	2.33	10.11	9.22	11.17	5.50
73E819	5.00	3.10	4.40	2.40	10.10	11.49	9.00	5.10
75E794	5.60	2.90	4.50	1.90	11.47	12.95	10.57	5.92
73E825	4.50	3.00	4.30	2.15	11.34	12.42	10.44	4.89
76E953	5.10	3.10	5.00	2.18	12.71	13.20	10.80	5.87
73E839	5.80	3.50	4.40	2.44	12.12	13.13	10.72	6.30
73E816	5.45	3.00	5.55	3.12	11.27	12.98	11.40	5.64
76E1037	5.20	2.70	4.90	2.24	11.29	13.84	10.60	7.24
76E1025	5.10	3.00	4.70	3.00	11.77	12.88	10.13	6.17
70C197	4.25	2.40	4.00	2.68	11.80	13.60	10.40	5.88
69B100	5.00	3.00	3.90	2.22	11.30	12.66	9.86	6.04
69B098	5.36	2.88	4.80	2.60	12.40	15.30	11.90	7.00
69B094	5.00	2.40	5.00	2.57	11.00	13.65	10.60	6.12
71B207	5.35	2.80	5.50	2.50	11.25	13.36	10.50	6.14
70B143	5.40	3.00	5.25	2.38	11.13	13.13	10.50	6.10
72C566	4.60	2.35	4.50	2.05	11.34	12.92	10.40	[6.15]
72C568	4.60	2.30	4.90	1.98	11.26	12.90	9.75	5.93
72D574	4.50	2.40	4.60	2.14	11.78	12.12	9.56	5.18

CAT	B20	B21	B22	B23	B24	V1	V2	V3
73E832	9.70	.	.	.33	.51	12.40	14.80	12.80
76E952	7.20	2.87	4.18	.61	.43	11.50	13.80	12.50
75E796	8.90	3.00	3.61	.40	.64	11.70	13.20	13.00
73E819	8.00	2.35	4.05	.30	.67	12.15	14.10	12.80
75E794	8.80	2.91	4.27	.40	.70	11.90	14.25	12.40
73E825	7.30	3.08	3.76	.57	.75	12.90	14.20	13.30
76E953	9.00	.	.	.39	.99	12.50	14.60	12.50
73E839	8.50	3.21	4.71	.49	1.18	12.10	14.90	12.90
73E816	7.00	2.97	4.66	.71	.52	12.00	14.95	11.80
76E1037	8.50	3.40	4.58	.57	.89	12.00	13.70	11.70
76E1025	8.30	3.10	4.53	.55	.70	12.50	14.70	13.10
70C197	10.50	2.80	4.30	.45	.80	12.40	14.50	12.60
69B100	10.50	2.80	4.50	.40	.42	11.60	12.80	11.00
69B098	10.60	3.05	5.00	.80	.75	13.90	15.70	13.60
69B094	10.00	2.98	4.30	.65	[.50]	12.00	13.90	12.90
71B207	9.40	3.34	5.00	.60	.75	12.25	14.20	14.30
70B143	9.50	2.90	4.57	.60	1.05	12.20	14.00	12.50
72C566	8.50	3.00	4.00	.75	.88	12.10	14.50	12.60
72C568	9.00	3.50	4.79	.55	.60	11.10	13.45	11.60
72D574	7.50	3.00	4.05	.60	.48	11.40	13.85	12.40

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CAT	V4	V5	V6	V7	V8	V9	V10	V11
73E832	10.70	13.50	11.14	12.10	10.00	[13.00]	9.00	6.25
76E952	10.88	12.90	11.12	11.10	9.10	13.00	9.01	6.40
75E796	11.10	13.50	12.34	11.00	8.76	12.70	9.70	5.32
73E819	11.25	13.40	11.80	11.50	9.47	12.60	9.64	5.58
75E794	10.75	12.30	11.39	12.10	9.45	12.25	9.32	5.76
73E825	11.50	12.70	11.36	13.20	10.90	13.10	10.18	7.48
76E953	11.06	13.30	11.61	11.90	10.00	12.90	9.18	5.55
73E839	11.36	13.80	12.71	11.70	9.39	12.80	9.54	6.46
73E816	10.48	12.90	11.37	11.80	9.58	13.40	8.87	7.41
76E1037	10.78	14.50	12.81	12.10	10.19	13.80	8.72	6.94
76E1025	11.47	13.40	11.49	11.00	9.13	13.80	9.90	6.08
70C197	11.10	13.00	11.45	12.80	9.98	12.85	9.20	7.48
69B100	10.05	12.50	11.30	13.00	9.57	11.70	8.20	7.00
69B098	11.82	14.40	12.54	12.00	9.55	13.75	10.34	6.70
69B094	11.05	12.20	10.92	11.50	9.36	13.20	9.14	5.56
71B207	12.14	12.40	11.12	12.00	10.07	14.05	10.30	6.90
70B143	10.85	14.00	12.21	11.40	9.46	13.15	8.68	5.84
72C566	10.88	12.10	10.70	[12.50]	[9.50]	12.95	9.30	6.72
72C568	10.05	10.80	9.84	[10.20]	[8.70]	11.75	8.75	5.90
72D574	10.95	13.30	11.90	10.80	8.42	12.65	9.36	6.26

CAT	V12	V13	V14	V15	V16	V17	V18	V19
73E832	6.60	5.31	5.40	7.05	19.50	12.12	9.52	8.70
76E952	7.20	3.98	4.20	6.38	16.70	10.60	8.35	7.89
75E796	4.95	4.83	6.00	8.00	22.50	10.60	9.03	8.21
73E819	5.70	5.98	6.10	7.32	19.00	11.05	9.12	8.40
75E794	6.00	5.96	6.00	7.79	22.50	12.45	9.44	8.55
73E825	8.00	4.89	5.00	[7.30]	[25.20]	11.98	9.29	8.76
76E953	6.00	5.85	6.00	.	.	12.28	8.72	8.17
73E839	6.70	4.95	5.00	[8.30]	[27.20]	11.90	9.90	8.90
73E816	7.90	3.83	4.00	[6.95]	[20.50]	12.26	9.16	7.65
76E1037	7.90	4.36	4.50	8.04	[24.00]	12.20	9.58	8.99
76E1025	6.50	4.48	4.70	[8.50]	[24.00]	12.30	9.45	8.60
70C197	8.60	4.04	4.20	9.46	26.50	12.70	9.60	8.23
69B100	8.00	4.80	5.00	7.50	22.50	11.30	9.08	7.90
69B098	7.20	4.90	4.80	9.00	26.50	12.94	10.00	8.80
69B094	6.00	5.18	5.50	9.50	29.00	11.85	9.57	8.76
71B207	7.40	4.37	4.60	9.60	27.00	11.70	9.65	8.90
70B143	6.40	4.75	5.00	7.50	26.50	11.47	9.50	9.03
72C566	7.90	[4.50]	[4.50]	8.20	[24.00]	10.94	8.94	8.00
72C568	6.60	[3.48]	[3.60]	[7.95]	[23.50]	10.82	8.87	8.25
72D574	6.60	3.60	4.20	8.20	23.50	10.87	9.12	8.45

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CAT	V20	V21	V22	V23	V24	F1	F2	F3
73E832	7.04	18.40	12.50	3.18	2.10	9.90	2.13	4.06
76E952	6.48	17.10	12.20	3.43	1.90	8.75	2.24	3.34
75E796	6.47	17.85	11.20	3.01	1.92	9.78	2.05	4.03
73E819	6.90	18.40	11.50	2.65	2.24	9.71	2.33	3.73
75E794	7.16	18.70	12.76	3.00	2.04	9.95	2.45	3.85
73E825	7.16	18.75	12.43	3.08	2.67	10.48	2.60	4.04
76E953	6.40	18.25	12.46	2.39	2.19	9.76	1.98	3.93
73E839	6.88	19.60	13.10	3.40	2.53	10.54	2.43	3.98
73E816	7.26	18.20	13.20	2.74	2.98	10.38	2.52	3.76
76E1037	7.53	19.10	13.04	2.47	3.10	9.76	2.46	3.68
76E1025	7.30	18.70	13.10	3.00	2.35	10.60	2.43	4.21
70C197	6.20	19.10	12.91	3.10	3.10	10.20	2.20	4.15
69B100	6.60	17.90	12.06	2.74	1.72	9.30	2.25	3.83
69B098	7.30	18.80	13.50	[3.00]	1.94	10.55	2.42	4.30
69B094	7.60	17.90	12.60	2.74	2.50	10.24	2.00	4.30
71B207	7.54	18.65	12.44	3.10	2.14	9.76	2.00	3.90
70B143	8.00	18.70	12.20	3.14	2.45	[9.80]	2.36	4.10
72C566	6.52	17.85	12.60	3.20	2.02	10.05	2.50	3.80
72C568	6.84	17.10	12.30	1.85	1.90	9.65	2.47	3.65
72D574	6.73	17.45	12.15	2.60	2.27	9.75	2.09	4.18

CAT	F4	F5	F6	F7	F8	F9	F10	F11
73E832	3.38	.15	11.09	11.80	10.07	8.92	2.28	4.99
76E952	3.36	.25	10.05	10.92	9.05	8.61	2.50	4.82
75E796	3.30	.20	10.82	11.96	9.89	8.67	2.40	4.85
73E819	3.47	.28	10.71	11.38	9.85	8.48	2.13	4.87
75E794	3.30	.10	11.12	12.18	10.11	9.84	2.40	5.41
73E825	3.44	.18	12.04	12.80	10.62	9.61	2.10	5.21
76E953	3.27	.34	11.28	12.32	9.90	8.85	2.52	5.00
73E839	3.65	.30	12.00	12.86	10.80	9.80	2.35	5.50
73E816	3.18	.40	12.26	13.12	10.47	9.92	3.20	6.13
76E1037	3.44	.40	12.02	13.04	9.93	9.45	2.40	5.33
76E1025	3.38	.25	12.40	13.52	10.73	9.42	2.40	5.30
70C197	3.64	.35	11.66	13.67	10.31	10.62	2.54	5.96
69B100	3.42	.17	11.00	12.10	9.51	9.02	2.75	5.26
69B098	3.25	.25	12.05	14.20	10.80	9.46	2.20	5.17
69B094	3.42	.30	12.30	14.10	10.46	9.35	2.40	5.24
71B207	3.34	.32	11.51	[13.50]	9.85	10.04	2.65	5.63
70B143	3.24	.42	[11.40]	.	10.04	[9.50]	2.15	5.02
72C566	3.71	.18	11.50	13.10	10.13	9.45	1.90	5.19
72C568	3.45	.05	11.34	12.54	9.85	[9.56]	2.15	5.30
72D574	3.37	.22	10.80	[12.40]	9.70	9.05	2.35	5.12

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CAT	F12	F13	F14	F15	F16	F17	F18	F19
73E832	6.00	4.92	2.24	.89	.60	8.40	4.64	5.43
76E952	5.78	4.33	2.21	1.09	.41	7.75	4.33	4.80
75E796	6.54	5.01	2.20	.88	.48	8.61	4.42	5.41
73E819	6.56	4.89	2.53	1.11	.50	8.20	4.99	5.23
75E794	7.02	5.44	2.28	.85	.44	8.14	4.34	5.00
73E825	6.82	5.29	2.51	1.04	.63	9.05	4.89	5.63
76E953	6.28	5.02	2.33	.88	.	8.60	4.60	5.41
73E839	7.52	5.86	2.80	.90	.67	8.70	4.86	5.40
73E816	7.08	5.57	2.44	1.09	[.59]	9.37	4.57	5.50
76E1037	7.15	5.54	[2.42]	1.10	.77	8.67	5.00	5.89
76E1025	7.02	5.28	2.80	1.10	.70	9.04	4.50	5.29
70C197	6.80	5.34	2.27	.52	.52	9.55	.	4.43
69B100	6.20	4.60	2.58	1.00	.90	8.70	3.92	4.87
69B098	6.43	4.95	2.32	1.10	1.05	9.70	4.84	5.73
69B094	7.12	5.13	2.30	.80	.84	9.32	4.95	6.06
71B207	7.80	5.62	2.65	.97	1.12	9.24	4.80	5.40
70B143	6.65	5.01	2.42	.63	.74	[9.10]	.	.
72C566	6.43	4.88	2.20	.75	.52	9.11	4.70	4.50
72C568	6.00	4.97	[2.55]	.84	.70	8.83	.	.
72D574	6.70	4.86	2.01	.63	.78	8.66	.	.

CAT	F20	F21	F22	F23	F24	F25	F26	F27
73E832	3.27	2.02	[9.30]	7.43	[10.20]	[9.20]	.80	.39
76E952	2.70	2.07	8.91	7.22	9.10	8.84	1.35	.42
75E796	3.22	2.10	8.20	7.27	9.10	8.19	.69	.40
73E819	3.45	2.15	8.70	7.84	9.50	8.47	.53	.34
75E794	3.19	2.64	9.30	7.30	9.60	9.16	[.70]	[.31]
73E825	3.50	2.20	8.40	7.63	9.60	8.50	.83	.54
76E953	3.41	1.97	8.74	6.92	9.60	8.52	1.68	.35
73E839	2.84	2.38	9.36	7.92	10.40	[9.00]	1.05	.41
73E816	3.71	2.26	10.30	7.67	10.70	9.85	.69	.42
76E1037	4.14	2.53	9.45	7.80	10.30	[9.00]	.94	.53
76E1025	3.65	2.27	10.20	7.58	10.50	10.24	1.35	.53
70C197	2.35	2.30	9.35	7.05	10.05	9.16	1.26	.45
69B100	3.25	1.90	9.20	6.68	9.20	9.14	.80	.39
69B098	4.00	2.32	9.70	7.65	10.60	10.00	.91	.46
69B094	4.10	2.40	9.70	7.87	10.50	9.66	1.23	.48
71B207	3.55	2.62	10.50	8.10	10.75	10.34	.88	.36
70B143	.	2.06	9.85	7.82	10.35	9.89	.	.
72C566	3.03	2.13	8.35	7.40	9.50	8.13	1.03	.48
72C568	.	2.42	9.20	7.12	9.80	9.54	.	.
72D574	.	1.97	8.95	6.88	9.40	8.72	.	.

PAN

CAT	M1	M2	M3	M4	M5	M6	M7	M8
19393369	[8.68]	3.89	12.20	4.10	3.28	6.26	1.60	4.29
1924861C	8.00	3.93	11.60	3.85	3.50	6.56	1.48	3.90
36772C	8.14	4.98	12.50	4.00	2.98	5.80	1.71	4.12
1939965C	8.39	4.27	12.50	4.88	3.44	6.38	1.66	4.24
1939957C	7.37	4.50	13.00	4.57	3.53	5.64	2.12	3.74
19393363	9.38	4.42	12.70	4.90	3.37	6.60	1.97	3.77
19393365	10.16	4.63	13.10	4.94	3.70	6.26	1.80	4.35
18641217	7.38	4.36	11.40	4.08	3.21	6.03	1.69	4.20
19393366	8.70	3.92	11.00	3.90	3.15	5.84	1.65	3.85
19393367	7.00	3.80	10.70	4.03	2.65	5.74	1.65	3.55
27141T	10.00	4.82	12.50	3.95	3.25	5.40	1.65	4.76
204132R	[8.90]	4.50	11.80	3.96	3.10	6.15	1.64	3.90
19393383	7.90	4.31	11.40	4.18	2.50	6.45	1.46	3.70
19687511	[7.84]	4.43	[11.50]	3.85	3.50	6.01	1.57	[3.40]
19393379	7.55	4.14	10.40	3.97	2.60	5.60	1.45	3.85
19393364	9.07	4.50	12.80	4.22	3.60	5.62	1.65	4.00
19393362	8.20	[4.80]	12.20	4.60	3.30	6.70	1.75	4.05
871212Z	9.56	4.29	13.40	5.16	4.00	6.90	1.80	3.95
19393377	8.97	4.32	11.60	4.70	2.70	6.85	1.55	4.05
19393385	8.55	4.40	12.20	4.40	3.60	6.12	1.16	4.05

CAT	M9	M10	M11	M12	P1	P2	P3	P4
19393369	5.65	2.62	2.57	6.67	6.28	3.65	6.90	5.90
1924861C	5.20	2.65	2.72	6.24	6.70	3.29	7.05	5.55
36772C	5.98	2.81	2.81	6.50	6.24	3.85	7.10	6.24
1939965C	5.64	2.81	2.87	6.80	6.49	3.76	7.40	5.56
1939957C	5.86	3.00	2.67	6.63	6.98	4.04	7.80	6.69
19393363	5.61	3.27	3.10	6.84	7.06	3.96	7.50	6.22
19393365	5.76	2.70	2.65	6.72	6.92	3.56	6.99	5.97
18641217	5.40	2.49	2.60	6.67	6.26	3.38	6.75	5.53
19393366	5.10	2.30	2.20	6.00	6.50	3.20	6.70	5.60
19393367	4.80	2.30	2.40	5.90	5.77	3.42	5.95	5.45
27141T	5.80	2.60	2.40	7.10	7.20	4.18	7.80	6.55
204132R	5.20	2.30	2.25	6.60	5.75	3.43	6.70	5.77
19393383	5.30	2.65	2.80	6.60	6.03	3.75	6.90	5.78
19687511	[5.50]	2.65	2.80	6.95	6.35	3.80	7.10	6.07
19393379	5.12	2.40	2.60	5.95	5.80	3.42	6.37	5.97
19393364	5.39	2.60	2.75	6.68	6.55	3.67	7.27	6.02
19393362	5.50	2.60	2.50	5.60	7.00	3.54	7.20	6.10
871212Z	5.30	3.00	3.10	6.90	8.10	3.63	8.00	5.94
19393377	5.31	2.70	2.60	6.20	6.50	3.56	6.80	5.66
19393385	5.50	2.60	2.50	6.95	6.15	3.75	6.80	6.16

PAN CAT	P5	P6	P7	P8	P9	B1	B2	B3
19393369	6.93	5.62	1.30	1.34	3.26	2.79	2.45	9.77
1924861C	6.65	5.47	1.01	1.24	3.24	3.20	2.50	10.26
36772C	.	6.20	1.20	1.33	3.51	[2.90]	[2.80]	10.80
1939965C	[5.80]	5.74	1.27	1.47	3.57	2.34	2.65	9.85
1939957C	[6.70]	6.35	1.30	1.27	3.65	3.10	2.50	9.96
19393363	7.62	6.26	1.56	1.58	3.95	2.80	2.27	10.86
19393365	7.17	5.96	1.10	1.28	3.31	2.85	2.22	10.40
18641217	6.91	5.58	1.31	1.34	3.30	2.50	2.27	8.92
19393366	6.74	5.40	1.10	1.12	3.50	2.23	1.97	8.75
19393367	6.30	5.30	1.00	.70	3.06	2.90	2.15	9.30
27141T	7.20	6.40	1.20	1.35	4.30	2.20	2.22	10.36
204132R	6.76	5.63	1.25	1.25	3.43	3.03	2.81	10.00
19393383	7.00	5.72	1.15	1.25	3.66	2.80	2.44	9.76
19687511	7.17	[5.80]	1.05	1.15	3.84	2.80	2.38	9.70
19393379	6.40	5.78	1.28	1.30	3.42	2.56	2.16	9.22
19393364	6.97	5.76	1.40	1.40	3.59	3.31	2.34	9.95
19393362	.	5.80	1.35	1.53	3.50	[2.70]	2.40	10.70
871212Z	7.28	5.95	1.35	1.40	3.90	2.72	2.28	11.40
19393377	6.40	5.57	1.20	1.30	3.59	3.10	2.56	10.32
19393385	7.02	[6.00]	1.10	1.00	3.14	[2.57]	[2.70]	9.78

CAT	B4	B5	B6	B7	B8	B9	B10	B11
19393369	6.36	5.69	4.41	2.60	4.00	4.80	2.70	2.46
1924861C	6.36	5.84	4.63	2.16	4.30	4.80	2.90	2.50
36772C	6.58	6.10	4.30	2.52	4.37	5.40	3.37	2.41
1939965C	6.45	5.93	4.24	2.56	4.11	5.20	3.03	2.18
1939957C	6.36	5.91	4.00	2.37	4.57	5.34	2.99	2.66
19393363	6.84	6.28	4.40	2.25	4.30	4.78	3.43	2.70
19393365	6.63	5.74	4.38	2.47	4.41	5.12	3.66	2.50
18641217	5.97	5.60	4.10	2.45	4.25	5.12	2.25	2.34
19393366	5.60	5.00	3.80	2.12	3.74	4.64	2.60	2.17
19393367	5.62	5.10	3.80	2.08	3.83	4.60	2.70	2.10
27141T	6.10	5.65	4.00	2.40	4.86	5.40	3.23	2.30
204132R	6.30	5.95	4.30	2.30	4.20	4.84	2.85	2.21
19393383	6.40	5.75	4.10	2.37	4.32	5.16	2.90	2.30
19687511	6.14	5.93	4.50	2.54	4.58	5.22	2.57	2.28
19393379	6.00	5.42	3.93	2.32	4.06	4.48	2.76	2.35
19393364	5.86	5.50	4.25	2.51	3.96	5.10	3.00	2.63
19393362	6.32	5.86	4.07	2.38	4.17	5.07	3.40	2.17
871212Z	6.85	6.15	4.72	2.60	4.48	5.27	3.64	2.58
19393377	6.50	6.24	3.80	2.58	4.60	5.14	3.24	2.10
19393385	5.90	5.35	4.00	2.26	4.33	5.04	2.94	2.50

PAN CAT	B12	B13	B14	B15	B16	B17	B18	B19
19393369	4.10	2.20	5.10	2.65	8.27	11.64	7.85	4.50
1924861C	4.30	2.30	5.10	2.50	7.90	12.22	8.10	5.72
36772C	4.50	2.10	4.90	1.72	8.54	11.84	8.57	[5.50]
1939965C	4.50	2.10	5.00	2.27	8.63	11.81	7.70	5.16
1939957C	4.80	2.20	5.50	2.20	8.14	12.20	8.10	4.82
19393363	5.00	3.10	5.20	2.98	9.30	12.10	8.66	5.46
19393365	5.15	2.65	5.30	2.91	8.30	12.38	8.68	4.67
18641217	5.00	2.30	5.20	2.70	7.72	11.18	6.55	3.63
19393366	4.70	2.45	5.05	2.15	8.30	10.85	6.57	3.97
19393367	4.55	2.50	4.70	2.20	7.82	10.70	8.05	5.15
27141T	5.30	2.73	5.40	2.77	8.50	11.90	8.20	5.50
204132R	4.60	2.00	5.20	2.60	7.94	11.67	7.80	4.05
19393383	4.70	2.50	5.10	2.50	8.40	11.20	9.00	5.75
19687511	4.82	2.32	5.50	2.65	8.63	11.74	9.42	6.05
19393379	4.13	2.58	4.70	2.67	7.20	10.72	7.70	5.40
19393364	5.07	3.00	5.10	2.63	7.37	11.50	8.84	5.75
19393362	4.70	2.20	5.30	2.85	9.90	13.25	8.13	6.57
871212Z	5.72	2.83	5.60	2.61	7.35	12.57	8.57	6.33
19393377	5.40	2.80	5.70	2.85	8.54	12.64	8.86	5.90
19393385	5.35	2.80	5.40	2.71	8.23	11.80	[8.30]	5.62

CAT	B20	B21	B22	B23	B24	V1	V2	V3
19393369	7.00	3.46	6.00	.10	.57	8.40	9.50	8.00
1924861C	6.70	3.40	5.50	.16	.64	7.60	10.10	7.70
36772C	6.50	4.45	6.04	.12	.47	8.70	10.00	8.10
1939965C	5.50	3.93	5.93	.20	.71	8.00	9.90	7.80
1939957C	5.10	4.13	6.67	.13	.41	8.50	10.30	7.50
19393363	5.80	3.67	6.30	.90	.34	8.60	10.00	8.50
19393365	11.50	3.12	5.63	.12	.51	7.75	9.95	8.30
18641217	7.70	3.07	5.53	.08	.40	8.40	9.80	7.70
19393366	9.00	3.10	5.13	.30	.60	8.60	9.30	7.10
19393367	8.50	3.14	4.92	.40	.45	8.17	9.20	7.90
27141T	8.00	3.43	5.83	.35	.85	7.70	9.66	7.90
204132R	7.00	3.90	6.17	.25	.50	8.11	9.70	7.70
19393383	7.00	3.40	5.70	.28	.42	8.30	9.48	8.60
19687511	7.60	4.00	6.14	.24	.60	8.20	9.94	8.20
19393379	6.10	3.07	5.20	.30	.42	7.93	8.83	7.30
19393364	6.50	3.60	6.02	.53	.58	8.13	8.97	7.80
19393362	8.30	3.42	5.90	.40	.45	8.60	10.26	8.50
871212Z	7.50	3.60	6.10	.40	.50	8.42	9.83	9.00
19393377	7.50	3.60	6.00	.48	.55	8.90	9.61	8.80
19393385	7.60	3.63	5.95	.30	.50	8.46	9.28	8.00

PAN CAT	V4	V5	V6	V7	V8	V9	V10	V11
19393369	7.41	6.10	5.86	6.00	5.23	8.60	5.47	1.71
1924861C	7.08	7.25	6.87	5.80	4.70	8.80	4.92	1.89
36772C	7.48	6.70	6.21	6.20	[5.20]	8.90	5.05	2.00
1939965C	6.85	6.50	6.02	6.90	5.80	8.60	4.20	2.71
1939957C	6.96	6.50	6.26	5.70	4.82	9.10	5.10	2.13
19393363	7.58	6.70	6.35	6.90	5.77	9.30	5.24	2.06
19393365	7.23	7.00	6.86	6.90	5.62	8.90	4.78	.
18641217	6.82	7.00	6.61	6.70	5.57	9.20	5.03	2.63
19393366	6.40	7.90	7.17	6.10	5.20	8.90	4.25	2.50
19393367	6.73	7.00	6.46	5.40	4.62	8.00	4.74	2.05
27141T	6.95	8.00	7.50	5.80	5.30	8.40	5.23	.94
204132R	6.85	5.70	5.32	6.50	5.45	8.30	4.80	2.85
19393383	7.50	6.00	5.67	6.50	5.36	8.75	5.25	1.90
19687511	7.16	6.50	6.27	6.70	5.30	8.45	5.17	2.93
19393379	6.60	5.90	5.59	5.50	4.80	8.30	5.01	2.06
19393364	6.83	6.00	5.65	6.00	4.96	8.15	4.95	2.05
19393362	7.55	6.70	6.30	[6.80]	[5.55]	9.00	5.64	[2.10]
871212Z	7.90	6.80	6.34	5.90	4.90	8.80	5.75	1.11
19393377	7.68	6.40	5.98	6.80	5.46	9.10	5.63	2.67
19393385	6.87	7.40	6.90	5.00	4.25	8.80	4.98	2.40

CAT	V12	V13	V14	V15	V16	V17	V18	V19
19393369	1.70	4.09	4.30	6.91	21.40	10.60	8.13	7.70
1924861C	2.90	3.42	3.70	7.23	21.60	10.60	8.60	8.40
36772C	2.00	[4.24]	[3.80]	6.65	18.80	11.00	8.70	8.36
1939965C	2.80	3.85	4.10	6.94	23.80	10.67	8.20	8.04
1939957C	2.30	3.16	3.20	7.90	25.00	10.52	9.09	8.82
19393363	2.30	4.22	4.60	7.64	25.00	11.66	9.45	9.10
19393365	.	5.08	5.50	8.31	27.50	10.69	8.95	9.04
18641217	2.70	3.72	4.10	6.81	23.20	10.20	8.36	8.03
19393366	2.60	3.34	3.50	6.80	20.50	9.15	7.80	7.60
19393367	2.00	3.10	3.40	6.54	19.50	9.40	8.00	7.83
27141T	1.00	4.47	4.80	7.70	23.00	10.40	8.95	[8.50]
204132R	3.00	3.30	3.50	5.83	18.00	10.30	8.23	7.93
19393383	2.00	4.20	4.50	8.00	23.20	10.00	8.50	7.92
19687511	3.00	3.37	3.70	7.11	20.06	9.66	8.30	7.94
19393379	2.00	3.32	3.50	6.14	18.00	9.05	8.07	7.80
19393364	2.10	3.40	3.90	7.80	24.00	9.97	8.30	8.17
19393362	2.30	[4.15]	4.50	8.63	26.00	10.54	8.74	8.50
871212Z	1.30	4.30	4.60	8.25	25.30	10.70	9.12	8.94
19393377	2.60	3.82	4.20	8.30	24.50	10.40	9.03	8.60
19393385	2.60	2.30	2.40	6.80	20.50	9.90	8.70	8.36

PAN CAT	V20	V21	V22	V23	V24	F1	F2	F3
19393369	7.13	12.70	11.10	2.40	2.20	8.77	2.24	3.58
1924861C	7.78	13.15	11.10	1.76	1.44	8.70	2.32	3.39
36772C	7.47	12.70	11.40	1.25	1.27	9.28	2.65	3.33
1939965C	7.38	12.70	11.15	2.65	2.86	8.67	1.83	3.40
1939957C	8.00	13.30	11.38	1.56	2.20	8.61	2.13	3.19
19393363	8.57	13.55	12.02	2.25	2.45	9.25	2.13	3.70
19393365	8.10	13.45	10.90	2.00	2.90	8.58	2.05	3.30
18641217	7.15	13.10	10.84	2.59	2.53	8.59	1.93	3.42
19393366	6.84	12.25	10.50	2.67	2.60	8.12	2.16	3.03
19393367	6.76	12.10	10.04	.72	.70	7.93	1.38	3.16
27141T	7.40	13.10	11.00	1.50	1.48	8.52	1.74	3.50
204132R	7.51	12.30	11.24	1.74	2.00	7.62	1.00	3.20
19393383	7.27	12.90	10.90	1.50	1.20	8.90	1.96	3.56
19687511	7.08	13.25	11.07	.90	.85	8.06	1.74	3.34
19393379	6.95	11.50	10.29	1.80	1.44	8.15	1.67	3.32
19393364	7.41	12.50	10.80	1.23	1.15	9.00	1.90	3.52
19393362	7.70	[13.70]	11.74	1.72	1.45	8.93	2.82	3.47
871212Z	8.24	13.60	11.55	1.60	1.50	8.96	2.10	3.54
19393377	8.30	13.60	12.00	1.65	2.14	8.70	1.93	3.33
19393385	7.50	12.30	11.33	1.60	1.68	9.38	1.88	3.90

CAT	F4	F5	F6	F7	F8	F9	F10	F11
19393369	3.56	.90	10.21	12.00	9.45	8.70	2.80	5.35
1924861C	3.50	.98	10.40	12.41	9.40	8.28	2.70	5.10
36772C	3.22	.72	11.73	11.90	9.60	8.92	3.20	5.50
1939965C	3.22	1.30	10.20	11.33	9.10	8.42	2.88	5.09
1939957C	3.51	.50	10.52	11.96	8.85	8.90	3.10	5.63
19393363	3.58	1.30	11.41	12.42	10.41	9.20	3.25	5.50
19393365	3.30	1.49	10.49	12.31	9.25	8.99	3.08	5.50
18641217	3.03	.83	10.20	11.24	9.27	8.52	3.03	5.16
19393366	3.04	.95	9.77	11.60	8.84	8.35	2.80	4.94
19393367	3.02	1.30	9.40	10.70	8.46	8.60	2.20	4.87
27141T	3.44	1.00	10.34	12.14	9.20	9.00	3.30	5.58
204132R	3.17	.75	9.78	11.97	8.34	8.43	2.80	5.00
19393383	3.80	1.10	10.37	11.77	9.37	8.56	3.00	5.14
19687511	3.17	1.03	[9.40]	11.65	8.55	[8.70]	2.85	5.08
19393379	3.33	.65	9.12	11.45	8.89	8.05	2.50	4.86
19393364	3.32	[1.05]	10.50	12.20	9.45	9.20	3.50	5.86
19393362	2.93	1.10	11.24	13.44	9.87	10.10	2.70	6.00
871212Z	3.30	1.30	10.45	13.47	9.74	9.39	3.83	6.08
19393377	3.62	1.05	10.70	13.14	9.16	9.14	2.75	5.30
19393385	3.58	.85	10.74	12.74	9.98	9.93	3.50	5.97

PAN CAT	F12	F13	F14	F15	F16	F17	F18	F19
19393369	8.42	6.51	3.06	1.10	.82	8.25	4.74	5.20
1924861C	8.17	5.72	2.60	.37	.57	8.28	5.00	5.73
36772C	7.61	5.30	2.90	[.16]	.84	8.54	4.87	5.38
1939965C	8.27	5.68	2.40	.58	.71	8.10	4.35	5.48
1939957C	10.26	7.31	2.90	1.22	.78	8.90	5.48	5.71
19393363	9.18	6.67	2.88	.83	1.00	9.00	5.01	6.04
19393365	7.67	5.50	2.61	.73	.61	9.02	5.21	5.81
18641217	7.30	5.13	2.69	.91	.73	8.31	4.63	5.32
19393366	6.77	4.38	2.52	.	.75	8.14	4.60	5.34
19393367	6.40	4.93	2.22	.40	.70	8.10	4.60	5.07
27141T	[9.00]	6.23	2.60	.	.86	8.84	5.30	6.20
204132R	7.42	5.44	2.47	.65	1.00	8.08	4.50	5.20
19393383	8.32	6.02	2.60	.	1.00	8.34	4.70	5.30
19687511	8.14	5.24	2.57	.62	.74	[8.20]	4.92	5.15
19393379	7.34	5.32	2.29	.	.74	7.73	4.85	[5.70]
19393364	8.72	6.16	2.92	.	.93	8.54	4.36	4.87
19393362	8.46	5.86	2.74	.	.70	9.23	5.30	5.70
871212Z	9.38	6.81	3.15	.	.93	9.07	5.40	6.14
19393377	8.00	6.04	2.72	.	.75	8.10	5.50	5.70
19393385	8.64	6.31	2.67	.72	1.10	9.20	5.12	5.60

CAT	F20	F21	F22	F23	F24	F25	F26	F27
19393369	3.69	2.78	12.60	6.88	9.40	12.66	.57	.43
1924861C	4.45	2.55	12.80	7.36	9.40	12.63	.71	.60
36772C	3.72	2.46	12.80	6.95	9.50	12.80	.82	.21
1939965C	3.38	2.90	13.23	6.77	9.30	13.05	.78	.23
1939957C	3.89	3.15	14.30	7.75	10.70	13.96	.92	.25
19393363	4.24	2.83	13.85	7.79	10.40	13.88	.55	.38
19393365	4.17	2.31	12.90	7.91	9.90	12.97	.77	.36
18641217	3.54	2.77	12.40	6.80	9.85	12.42	.85	.33
19393366	3.93	2.58	12.00	6.57	8.90	12.00	.80	.27
19393367	3.00	2.72	11.10	6.85	8.80	11.05	.97	.23
27141T	4.12	3.08	13.60	7.30	9.90	13.60	1.00	.30
204132R	4.93	2.84	12.60	6.82	8.90	12.57	.76	.39
19393383	3.93	2.39	12.30	6.75	9.70	12.31	.94	.22
19687511	3.60	2.56	12.80	6.82	9.30	12.98	.67	.20
19393379	3.90	2.62	11.55	6.94	9.10	11.44	.61	.18
19393364	2.90	2.43	13.00	6.94	9.15	13.10	.64	.21
19393362	3.37	3.43	13.43	7.37	10.00	13.33	.78	.36
871212Z	4.54	3.26	14.50	7.71	10.50	14.30	.85	.33
19393377	4.13	2.90	12.70	7.72	9.90	12.90	.54	.46
19393385	3.64	2.62	12.60	7.37	9.60	12.60	.66	.30

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CAT	M1	M2	M3	M4	M5	M6	M7	M8
1939913C	10.60	4.80	17.10	7.35	5.25	11.57	2.35	4.23
367141C	12.35	4.75	18.20	6.93	6.70	11.40	2.76	4.85
1939915C	11.60	4.92	15.50	7.23	4.75	10.90	2.27	4.84
48435C	12.60	5.28	17.00	7.76	4.30	12.31	2.38	5.20
1939912C	9.94	4.88	15.00	7.40	[4.90]	12.89	2.93	3.51
1939914C	9.45	4.38	13.00	4.99	4.35	9.05	2.22	3.57
1939925G	10.68	4.28	12.80	5.34	3.80	9.44	2.60	3.70
1939927G	9.20	4.62	13.60	5.48	3.70	8.53	2.33	4.70
1939929G	10.82	4.70	16.25	6.90	4.80	11.60	2.50	3.90
1939934G	8.53	4.64	13.95	5.38	3.70	9.07	2.42	4.60
1939933G	7.63	4.24	13.30	4.89	3.30	7.93	2.15	4.10
18571123	10.30	4.44	14.10	5.51	4.15	9.80	2.15	4.80
19483312	8.80	4.62	13.90	5.10	3.90	10.10	2.40	4.50
86758C	9.90	4.87	13.00	5.18	3.75	9.52	2.03	4.88
1939924G	12.90	5.20	17.10	7.88	4.65	13.78	2.70	4.80
2311296Z	12.00	4.67	15.40	5.87	5.40	11.20	2.36	4.70
1948541Z	12.10	4.72	15.70	6.90	4.99	13.20	2.62	5.07
25141Z	10.54	5.12	17.80	7.76	5.15	11.65	2.65	4.90
2311298Z	9.66	4.63	15.40	5.90	4.30	10.07	2.24	4.60
1939922Z	9.30	4.02	13.25	5.29	4.15	8.90	2.51	[4.40]

CAT	M9	M10	M11	M12	P1	P2	P3	P4
1939913C	6.39	4.20	4.50	9.55	10.50	4.16	10.90	7.54
367141C	6.77	4.35	3.85	9.66	10.80	4.17	11.62	7.50
1939915C	6.63	3.65	3.90	8.84	10.30	4.24	10.97	7.48
48435C	6.84	3.85	4.40	9.73	10.45	3.92	10.74	6.94
1939912C	6.60	4.30	3.97	[9.55]	11.02	4.50	10.70	7.50
1939914C	6.24	3.74	3.47	8.50	8.03	4.00	8.90	7.10
1939925G	6.37	3.90	3.73	8.80	8.70	4.00	9.47	7.08
1939927G	6.58	3.50	3.50	8.45	8.60	3.55	8.60	6.78
1939929G	6.59	4.10	3.90	9.00	9.31	4.30	9.95	7.47
1939934G	6.84	3.50	3.30	8.02	8.00	3.51	8.90	6.70
1939933G	6.32	2.95	2.65	8.15	7.32	3.40	9.10	6.15
18571123	6.94	3.30	3.50	8.77	8.92	4.12	9.42	6.97
19483312	6.44	3.50	3.55	8.50	8.33	3.93	8.70	7.09
86758C	5.99	3.40	3.45	7.80	8.37	3.72	8.10	6.25
1939924G	6.93	4.15	4.40	10.52	11.00	4.25	11.46	7.38
2311296Z	6.93	4.05	4.10	9.00	8.22	3.83	9.10	6.90
1948541Z	6.70	4.10	4.50	9.87	11.64	4.79	11.47	7.80
25141Z	6.76	4.30	4.38	10.61	10.90	.	11.47	7.60
2311298Z	6.62	3.92	3.90	[8.35]	9.14	4.01	9.20	7.06
1939922Z	6.12	3.30	3.25	8.06	8.90	3.46	9.30	6.23

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CAT	P5	P6	P7	P8	P9	B1	B2	B3
1939913C	9.93	7.16	2.15	2.10	3.74	3.63	3.00	14.00
367141C	10.60	7.34	1.90	1.85	4.64	3.39	2.80	14.14
1939915C	.	7.52	1.38	1.64	4.00	.	.	15.00
48435C	.	6.86	1.55	1.68	3.82	3.28	3.10	13.50
1939912C	9.96	7.24	1.86	1.97	4.30	3.60	3.36	15.59
1939914C	8.79	6.78	2.20	1.93	4.34	[3.00]	[2.36]	11.81
1939925G	9.05	6.84	2.20	2.30	4.22	3.25	2.90	12.04
1939927G	8.90	6.62	1.35	1.58	3.34	2.90	2.57	11.44
1939929G	9.70	.	1.86	1.95	4.10	3.10	3.15	14.32
1939934G	8.80	6.62	1.50	1.33	3.44	3.25	3.12	12.20
1939933G	[8.50]	5.90	1.50	1.62	3.40	2.93	2.60	11.36
18571123	8.84	6.77	1.52	1.98	4.12	2.92	2.42	12.85
19483312	9.10	6.75	1.51	1.70	4.39	3.31	2.58	11.18
86758C	8.02	.	1.75	1.80	3.43	3.13	2.52	11.92
1939924G	11.25	7.30	1.97	2.25	4.92	3.08	3.07	14.33
2311296Z	9.27	6.91	1.83	2.02	3.61	3.63	3.06	13.26
1948541Z	10.92	7.64	1.88	1.68	5.41	3.40	3.16	14.37
25141Z	10.49	7.55	2.30	2.08	3.77	3.46	3.19	13.13
2311298Z	8.39	6.98	1.17	1.90	3.96	3.40	2.93	12.21
1939922Z	9.12	6.13	1.57	1.45	3.70	[3.00]	2.71	11.81

CAT	B4	B5	B6	B7	B8	B9	B10	B11
1939913C	8.18	7.00	5.60	3.12	4.95	6.14	4.24	3.30
367141C	8.00	6.70	4.80	2.95	5.15	5.88	5.17	2.85
1939915C	9.43	7.56	5.60	3.75	5.57	6.20	5.10	3.20
48435C	7.90	6.70	4.98	3.14	4.88	5.64	4.33	2.77
1939912C	8.86	7.38	5.95	3.56	5.75	6.16	5.30	3.35
1939914C	7.60	6.17	4.43	2.50	5.14	5.91	3.91	2.75
1939925G	7.53	6.78	5.02	2.74	4.93	5.68	3.80	3.00
1939927G	7.95	6.02	4.70	2.80	5.20	5.70	3.48	2.68
1939929G	8.88	6.90	5.20	3.45	6.30	7.15	4.82	3.24
1939934G	8.10	7.32	4.98	3.25	5.84	6.27	3.80	2.78
1939933G	7.56	6.70	4.70	3.10	5.14	5.20	3.40	2.84
18571123	8.03	6.38	4.60	2.62	5.04	5.70	4.14	2.87
19483312	7.02	5.98	4.95	2.49	4.67	5.94	3.28	3.05
86758C	7.17	5.48	4.30	2.61	4.80	5.45	4.34	2.47
1939924G	8.85	7.04	5.70	3.10	5.46	6.12	4.34	3.50
2311296Z	8.00	6.70	4.57	3.37	5.45	6.20	4.53	3.04
1948541Z	9.01	7.40	5.63	3.25	5.62	5.96	4.61	2.88
25141Z	7.97	7.05	5.36	3.06	5.27	6.17	3.87	3.47
2311298Z	7.76	6.33	4.44	2.82	5.38	5.70	4.31	2.97
1939922Z	7.68	6.23	3.91	2.70	4.93	5.40	4.06	2.05

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CAT	B12	B13	B14	B15	B16	B17	B18	B19
1939913C	6.70	4.00	7.50	3.64	13.74	15.93	11.86	8.38
367141C	7.80	4.70	7.70	3.30	13.70	16.00	12.00	7.77
1939915C	7.40	4.60	[7.50]	[3.40]	12.37	16.30	12.85	7.84
48435C	7.40	3.90	7.90	3.70	13.72	15.90	[12.50]	8.42
1939912C	6.70	4.30	6.50	3.59	13.42	17.00	13.20	8.88
1939914C	5.20	3.20	5.80	2.00	11.00	12.55	10.63	[6.35]
1939925G	5.50	3.70	5.40	2.90	10.60	13.55	10.70	7.12
1939927G	4.95	2.90	5.60	2.90	8.14	12.33	9.60	6.36
1939929G	7.00	4.25	7.50	3.52	11.00	15.28	11.80	7.30
1939934G	5.50	2.90	6.20	3.10	10.33	13.62	11.00	6.86
1939933G	6.00	3.50	5.50	2.80	10.24	12.50	10.20	6.30
18571123	5.50	3.05	6.55	3.37	10.64	13.77	10.60	7.20
19483312	5.70	3.00	6.05	2.62	8.99	12.64	9.40	6.25
86758C	5.75	3.70	5.50	2.94	8.83	12.30	10.30	6.27
1939924G	7.00	4.00	7.60	3.40	14.04	16.90	12.40	9.30
2311296Z	5.40	3.90	5.90	3.41	13.43	16.20	11.30	7.90
1948541Z	6.30	3.70	7.85	3.94	12.95	16.50	13.13	8.61
25141Z	7.00	3.70	8.85	4.17	14.20	15.76	11.17	8.31
2311298Z	6.00	3.00	7.15	3.38	10.50	14.78	11.20	7.97
1939922Z	5.00	2.90	[5.50]	[2.91]	11.07	12.58	9.72	7.00

CAT	B20	B21	B22	B23	B24	V1	V2	V3
1939913C	13.10	5.56	8.82	.88	1.30	9.50	11.00	11.50
367141C	13.70	5.16	8.24	.50	.90	8.34	9.65	12.00
1939915C	12.70	5.36	8.55	1.05	1.10	8.40	9.50	12.50
48435C	13.60	5.10	8.37	1.40	1.10	7.10	9.30	11.00
1939912C	15.60	5.46	8.35	.51	2.04	8.00	11.30	11.00
1939914C	8.00	5.05	6.81	.24	1.10	8.00	9.90	6.30
1939925G	10.00	4.50	6.78	.45	1.25	8.10	10.50	8.50
1939927G	7.80	3.95	6.23	.60	1.50	8.30	10.60	9.20
1939929G	11.20	5.18	8.61	.32	1.25	8.15	11.30	10.60
1939934G	9.00	4.15	6.95	.17	1.25	8.10	10.70	8.80
1939933G	9.30	4.20	6.71	.18	1.10	[8.40]	11.00	8.65
18571123	8.60	3.95	6.95	.52	1.48	7.80	10.30	9.40
19483312	9.90	4.10	6.21	.70	1.10	8.00	10.15	9.60
86758C	8.10	3.52	6.39	.52	1.25	7.50	9.50	8.50
1939924G	13.60	5.60	8.61	.70	1.40	8.20	10.10	12.30
2311296Z	11.60	4.30	6.55	.70	1.54	8.00	11.10	9.40
1948541Z	13.20	4.48	7.72	.39	1.12	8.80	11.20	10.00
25141Z	14.20	5.45	9.30	.63	1.23	8.20	10.30	9.90
2311298Z	9.80	4.17	7.25	.61	1.35	7.65	10.50	10.00
1939922Z	9.00	3.27	5.80	.50	.91	8.00	9.75	8.10

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CAT	V4	V5	V6	V7	V8	V9	V10	V11
1939913C	9.30	7.50	7.42	12.40	7.00	10.10	5.88	3.00
367141C	10.15	6.70	6.63	10.40	7.00	10.60	7.03	2.31
1939915C	10.14	6.80	6.60	.	.	[10.90]	6.70	4.50
48435C	9.25	7.20	7.11	14.30	6.60	10.65	5.80	3.10
1939912C	8.21	10.00	9.17	8.40	8.50	11.50	5.68	2.13
1939914C	5.56	9.50	9.00	[6.50]	[6.00]	9.80	5.43	1.76
1939925G	7.80	7.60	6.84	8.20	6.94	9.70	5.60	2.32
1939927G	7.83	7.70	7.36	6.90	5.81	9.70	5.32	1.50
1939929G	8.66	8.70	8.45	12.20	6.20	10.70	5.70	4.80
1939934G	8.12	8.00	7.63	7.20	6.08	9.60	5.74	1.73
1939933G	8.26	4.70	4.51	9.35	7.10	9.20	6.50	2.83
18571123	8.07	8.80	8.55	7.20	6.40	10.50	5.69	1.25
19483312	8.65	7.90	7.50	7.00	5.95	9.10	6.01	1.10
86758C	7.84	7.20	6.71	7.85	6.27	9.35	5.58	1.21
1939924G	10.76	8.30	8.23	[6.50]	7.40	10.60	6.07	4.83
2311296Z	8.50	7.10	7.01	[7.30]	6.77	9.70	5.53	2.18
1948541Z	9.08	8.00	7.07	[5.20]	7.20	11.60	6.46	4.57
25141Z	8.50	6.60	6.10	[6.20]	7.05	10.60	5.48	3.95
2311298Z	8.79	7.00	6.55	8.10	6.38	9.90	6.60	2.02
1939922Z	7.47	7.20	7.00	8.50	6.65	[9.70]	5.15	2.07

CAT	V12	V13	V14	V15	V16	V17	V18	V19
1939913C	5.10	7.40	7.50	12.04	40.50	13.40	11.23	11.20
367141C	3.70	6.62	6.90	11.40	36.00	13.70	11.50	11.64
1939915C	6.60	.	.	12.50	41.30	14.10	12.98	12.54
48435C	6.40	7.60	7.80	11.70	40.00	13.25	10.80	10.30
1939912C	2.70	10.00	10.20	11.64	43.50	14.96	11.80	12.63
1939914C	1.90	[4.70]	[5.00]	8.95	27.70	11.60	9.93	9.72
1939925G	3.00	5.23	4.90	9.09	28.20	12.03	9.54	9.65
1939927G	1.60	5.13	5.40	9.32	26.70	11.30	9.74	9.48
1939929G	6.30	7.55	7.80	11.31	39.00	14.00	12.13	12.04
1939934G	1.90	5.18	5.30	9.14	26.80	11.80	10.30	9.55
1939933G	3.00	5.07	5.35	8.52	24.00	11.88	9.63	9.77
18571123	1.40	5.77	5.90	9.36	30.00	12.10	10.43	10.16
19483312	1.40	5.56	5.80	8.91	30.30	10.80	10.16	9.45
86758C	2.00	5.16	5.20	8.95	27.50	11.00	9.94	9.41
1939924G	5.50	11.00	11.50	12.61	41.00	13.95	12.50	11.60
2311296Z	5.30	6.76	7.00	10.77	34.10	13.50	10.26	10.15
1948541Z	6.10	9.20	9.90	12.13	40.50	13.80	10.85	10.50
25141Z	8.10	9.96	10.10	12.55	36.40	13.00	11.90	11.46
2311298Z	2.30	5.84	6.00	8.98	27.80	12.21	10.44	10.38
1939922Z	2.60	6.04	6.10	9.17	28.50	10.95	9.51	8.87

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CAT	V20	V21	V22	V23	V24	F1	F2	F3
1939913C	11.25	19.30	14.00	2.20	1.96	11.60	2.40	4.50
367141C	11.52	18.10	14.40	2.40	2.52	11.98	2.60	4.72
1939915C	11.91	21.00	14.60	2.27	2.20	12.70	2.77	5.08
48435C	10.55	19.10	14.25	2.43	2.29	10.82	2.95	4.15
1939912C	12.70	22.10	15.10	2.35	2.48	11.32	1.98	4.90
1939914C	8.52	15.00	11.74	1.34	1.30	9.78	1.58	4.06
1939925G	9.25	15.40	12.15	1.48	1.37	9.98	2.00	3.96
1939927G	8.79	14.80	11.62	1.50	1.65	9.81	2.03	4.05
1939929G	11.53	20.60	14.40	1.42	2.40	11.60	2.75	4.54
1939934G	8.92	15.90	12.70	2.00	1.94	9.64	1.53	4.26
1939933G	8.50	15.00	11.97	1.40	1.66	9.15	1.59	3.79
18571123	8.60	16.40	12.60	2.30	2.33	10.07	1.79	4.16
19483312	8.61	16.10	11.54	1.52	1.30	10.04	1.93	4.15
86758C	8.58	15.10	11.30	1.48	1.75	9.84	1.77	4.10
1939924G	11.94	21.80	14.80	2.00	2.46	11.18	2.25	4.67
2311296Z	9.06	18.10	13.90	1.50	2.30	11.13	1.96	4.29
1948541Z	10.61	19.70	14.50	2.95	2.09	11.51	2.99	4.11
25141Z	11.14	17.05	13.90	1.75	1.65	10.70	2.25	4.28
2311298Z	9.15	16.50	12.82	1.98	1.79	10.28	2.00	4.13
1939922Z	8.20	15.20	11.50	.88	1.30	9.13	1.25	3.94

CAT	F4	F5	F6	F7	F8	F9	F10	F11
1939913C	4.60	2.80	14.77	17.00	12.60	11.74	5.10	7.84
367141C	4.30	2.30	15.03	17.30	13.04	13.46	[6.00]	9.14
1939915C	4.40	2.95	15.64	18.70	13.30	13.08	6.00	9.30
48435C	3.82	2.33	14.60	17.50	11.80	12.76	6.00	8.80
1939912C	4.51	2.26	15.03	18.75	12.03	13.50	[5.50]	8.70
1939914C	3.94	1.40	12.60	13.73	10.36	10.97	[5.00]	7.41
1939925G	4.33	1.50	12.20	13.76	10.24	10.31	4.10	6.35
1939927G	4.57	1.70	12.16	13.16	10.28	10.84	4.20	7.00
1939929G	4.38	2.80	15.14	16.90	12.55	12.77	[4.30]	7.70
1939934G	3.70	1.45	12.94	14.43	10.20	11.50	4.35	7.15
1939933G	3.72	1.30	11.58	13.20	9.80	10.07	4.05	5.96
18571123	3.87	1.90	12.47	14.40	10.50	11.66	4.00	7.05
19483312	3.84	2.05	12.30	13.85	10.48	10.38	4.30	6.70
86758C	4.03	1.75	12.55	13.34	10.60	10.72	3.80	6.55
1939924G	3.90	2.95	15.30	17.60	13.06	13.34	[5.00]	8.30
2311296Z	4.76	2.58	13.99	16.20	11.46	10.81	[5.20]	7.18
1948541Z	4.24	2.30	15.28	17.10	13.00	12.77	[5.00]	8.10
25141Z	3.70	2.45	14.12	17.05	10.63	13.28	[5.30]	8.12
2311298Z	3.79	1.96	12.86	14.30	10.61	11.62	4.00	6.95
1939922Z	3.94	1.85	12.03	13.53	9.70	10.40	3.50	6.38

GORILLA

CAT	F12	F13	F14	F15	F16	F17	F18	F19
1939913C	12.25	10.26	3.22	.62	1.60	11.74	7.00	8.40
367141C	11.10	9.00	3.60	.77	1.10	12.94	6.90	8.20
1939915C	11.50	9.61	4.15	.73	.83	13.78	8.22	9.35
48435C	10.63	9.14	3.47	.54	1.00	12.84	5.63	7.20
1939912C	13.50	12.20	4.46	.72	1.95	13.21	7.90	9.28
1939914C	10.51	9.15	3.81	.24	.61	10.75	6.18	7.16
1939925G	11.20	9.14	3.42	.	.62	10.10	5.90	6.70
1939927G	10.69	9.00	3.58	.66	.65	10.64	5.77	6.14
1939929G	[12.30]	10.05	3.65	1.05	.80	12.14	7.33	8.63
1939934G	10.44	8.65	3.30	.81	.76	11.34	6.10	6.40
1939933G	10.54	8.97	3.43	.49	.65	11.05	5.70	6.00
18571123	10.40	8.40	3.50	.35	.69	11.45	6.30	7.75
19483312	10.90	9.20	3.38	.54	.97	10.38	6.39	7.23
86758C	10.02	8.65	3.05	.12	.63	10.40	6.04	6.80
1939924G	11.85	10.11	4.03	.47	1.00	12.48	7.30	8.40
2311296Z	15.58	14.35	3.36	.41	1.26	10.74	6.33	6.57
1948541Z	13.94	11.53	3.92	.96	.72	12.54	7.15	7.90
25141Z	13.20	11.47	3.93	.66	.82	12.84	7.90	8.28
2311298Z	11.10	9.34	3.38	.57	.86	11.29	6.15	[7.40]
1939922Z	10.64	8.65	2.91	.95	.82	10.04	5.63	6.20

CAT	F20	F21	F22	F23	F24	F25	F26	F27
1939913C	6.58	3.90	19.70	9.40	13.40	20.45	1.90	.58
367141C	6.70	4.42	19.85	10.10	14.10	19.80	2.00	.77
1939915C	7.06	4.44	[19.50]	11.10	14.60	19.90	2.40	1.05
48435C	5.72	4.14	19.15	8.64	13.80	19.05	1.60	.97
1939912C	6.87	4.92	19.70	11.75	13.60	20.10	1.64	1.00
1939914C	4.36	3.16	[15.35]	8.34	[11.90]	[15.63]	1.70	.55
1939925G	4.95	3.05	16.25	8.50	11.10	16.20	1.30	.40
1939927G	4.30	3.28	15.00	8.43	11.10	15.13	1.57	.55
1939929G	6.20	4.49	18.25	10.50	13.40	.	1.83	.72
1939934G	3.88	3.80	15.63	8.58	11.80	15.44	1.62	.48
1939933G	4.25	3.08	14.49	8.36	11.30	14.50	1.27	.49
18571123	4.41	3.50	16.10	8.43	13.02	16.20	1.65	.64
19483312	5.19	3.57	14.90	8.85	11.70	15.07	1.30	.67
86758C	4.28	3.81	14.60	8.16	11.75	14.84	1.47	.34
1939924G	6.90	4.66	20.65	10.86	15.50	20.80	1.64	.82
2311296Z	5.92	4.64	15.35	8.47	13.20	15.37	1.50	.70
1948541Z	6.53	5.02	19.70	9.43	14.80	19.84	1.97	1.00
25141Z	6.50	4.91	21.10	10.18	15.17	21.50	1.90	.92
2311298Z	4.20	3.75	16.65	8.87	13.38	16.97	1.55	.69
1939922Z	4.20	3.05	[14.90]	8.07	11.70	[14.70]	1.50	.67

PONGO

CAT	M1	M2	M3	M4	M5	M6	M7	M8
1948763U	10.18	5.44	14.30	5.99	4.80	9.50	2.53	3.93
19761427	9.40	4.61	12.80	5.10	4.35	8.51	1.97	4.51
19761415	8.23	4.40	12.40	5.06	4.33	8.58	2.27	4.47
19761431	[9.86]	5.30	15.35	6.44	5.40	9.90	2.38	4.66
18443301	11.44	5.41	15.15	6.80	4.60	9.44	3.20	4.50
19761430	8.84	4.29	12.40	4.49	3.25	7.62	2.18	4.36
19761418	8.88	4.30	12.75	4.54	4.25	7.82	2.43	4.16
19761422	9.23	4.28	12.00	4.41	4.65	7.87	1.94	4.20
18561182	8.74	4.06	13.80	4.89	4.90	8.34	2.30	4.33
19761435	8.80	4.78	13.25	5.29	3.80	8.30	2.45	4.46
79112121	8.63	4.44	12.30	4.93	4.30	9.04	2.46	4.20
19861119	8.84	4.26	11.80	4.33	4.10	7.88	2.31	4.40
921153B	13.30	5.50	17.50	6.65	5.55	10.84	2.73	4.90
19761426	9.95	3.95	14.60	5.54	4.75	9.90	2.10	3.90
19761440	10.83	5.10	14.20	5.47	4.55	11.36	2.00	5.10
19761428	10.00	4.67	16.80	6.57	5.50	9.82	2.60	4.42
185231U	11.53	5.90	15.20	6.55	4.85	11.37	2.44	4.60
1948761	7.78	4.36	12.10	5.22	3.20	7.75	2.44	4.07
19861100	8.10	3.86	11.80	4.45	4.05	8.57	2.24	4.10
19861113	9.80	4.78	13.90	5.45	4.00	9.33	2.33	4.58

CAT	M9	M10	M11	M12	P1	P2	P3	P4
1948763U	6.21	3.80	4.00	8.25	8.24	4.51	9.20	7.44
19761427	5.71	3.20	3.70	7.10	7.04	3.56	8.29	6.55
19761415	5.76	3.40	3.25	7.84	6.99	3.48	8.09	6.03
19761431	6.31	4.10	3.90	8.22	8.20	4.05	8.96	6.83
18443301	6.83	3.70	3.68	8.62	8.16	4.33	9.06	7.23
19761430	5.82	3.30	3.15	7.54	6.81	3.82	8.00	6.27
19761418	5.62	3.20	2.93	7.67	6.94	3.68	7.88	6.40
19761422	5.95	3.60	3.52	7.22	6.37	[3.93]	7.40	6.54
18561182	6.41	3.60	3.45	8.59	7.25	3.45	8.14	6.30
19761435	6.52	3.40	3.50	[8.50]	7.07	3.86	8.12	6.55
79112121	5.80	4.10	4.05	7.08	6.85	3.75	7.70	6.44
19861119	5.75	3.20	3.35	7.50	6.30	3.44	7.78	5.98
921153B	6.77	4.50	4.10	8.68	8.60	4.32	9.50	7.67
19761426	5.74	3.70	3.60	8.32	8.06	4.14	9.10	7.07
19761440	6.55	3.75	4.10	8.00	8.14	4.84	8.80	7.57
19761428	6.47	4.00	4.25	8.90	8.60	4.15	9.53	7.50
185231U	6.30	4.25	4.95	[9.05]	8.90	4.80	9.53	7.72
1948761	5.81	3.05	2.85	7.20	6.46	3.43	7.22	6.25
19861100	5.72	3.35	3.25	7.17	6.44	3.90	7.31	6.58
19861113	6.44	3.15	3.20	8.06	7.67	4.33	8.28	6.92

PONGO

CAT	P5	P6	P7	P8	P9	B1	B2	B3
1948763U	9.28	7.32	1.38	1.50	4.43	3.22	2.42	12.12
19761427	8.04	6.22	1.46	1.59	3.61	2.45	2.48	11.25
19761415	[8.00]	6.06	1.30	1.06	3.80	3.25	3.00	10.67
19761431	8.74	6.75	[2.22]	2.14	4.30	3.10	2.57	13.47
18443301	9.51	7.13	1.20	1.43	4.88	2.90	2.29	12.48
19761430	8.25	6.32	2.00	1.47	3.51	3.72	2.64	10.04
19761418	[7.80]	6.20	1.40	1.32	3.61	[3.00]	.	10.40
19761422	7.51	6.36	1.50	1.31	3.58	[3.00]	2.14	10.48
18561182	8.85	6.20	1.91	1.57	3.22	3.16	2.78	11.07
19761435	8.71	.	1.75	1.70	3.67	2.76	[2.60]	11.13
79112121	.	6.30	1.75	1.55	3.63	2.97	2.33	11.35
19861119	8.15	5.85	1.50	1.40	3.20	3.21	2.94	9.97
921153B	9.06	7.25	1.49	1.72	4.74	2.72	2.48	13.35
19761426	9.00	6.94	1.70	1.88	3.78	3.46	[2.40]	11.15
19761440	8.32	7.48	2.15	1.90	4.54	3.87	2.62	11.96
19761428	9.00	6.84	2.10	2.20	3.90	[3.00]	2.57	11.40
185231U	8.87	7.50	2.50	2.10	4.92	3.64	2.86	13.25
1948761	7.30	6.12	1.10	1.00	3.40	2.58	2.34	9.84
19861100	7.55	6.29	1.00	1.01	4.03	3.37	2.70	10.80
19861113	8.20	6.82	.95	1.28	3.90	3.30	2.30	11.50

CAT	B4	B5	B6	B7	B8	B9	B10	B11
1948763U	8.26	7.70	5.58	2.86	4.77	5.45	3.31	3.14
19761427	6.94	6.24	4.57	2.50	4.10	5.24	3.42	2.99
19761415	7.74	6.88	4.95	2.80	4.50	4.55	2.92	2.70
19761431	8.50	7.32	6.01	3.13	4.81	5.63	3.62	3.25
18443301	7.20	6.50	5.00	2.71	4.50	5.47	3.91	3.00
19761430	6.94	5.55	4.54	2.95	4.20	5.68	3.12	2.37
19761418	7.50	6.85	5.02	2.83	4.45	4.96	3.00	2.62
19761422	6.87	6.42	4.65	2.37	4.15	5.05	2.94	2.32
18561182	7.15	6.65	4.70	2.54	4.25	4.83	3.36	2.80
19761435	7.57	6.53	4.82	2.61	4.14	4.67	3.08	2.90
79112121	7.32	6.14	4.43	2.75	4.20	4.88	3.65	2.77
19861119	6.95	6.02	4.30	2.36	3.97	4.97	2.95	2.40
921153B	8.38	7.60	5.85	3.10	5.25	5.60	3.65	3.25
19761426	[7.50]	6.32	5.10	2.70	4.40	4.86	3.46	3.18
19761440	7.05	6.14	4.68	2.99	4.54	6.55	3.55	2.44
19761428	7.34	6.65	4.90	3.05	4.87	5.53	3.41	2.87
185231U	7.93	6.45	5.22	2.84	4.84	5.95	4.26	3.10
1948761	6.47	5.65	4.56	2.50	3.90	4.78	2.75	2.45
19861100	7.56	6.44	4.40	2.73	4.07	5.37	3.26	2.63
19861113	7.50	5.90	4.87	3.00	4.75	5.90	3.30	2.50

PONGO

CAT	B12	B13	B14	B15	B16	B17	B18	B19
1948763U	6.20	3.10	6.50	3.09	11.63	13.41	9.90	6.80
19761427	5.40	2.50	5.75	2.68	10.47	12.38	9.80	6.72
19761415	5.20	2.10	5.60	2.52	10.71	12.05	9.20	6.41
19761431	6.20	2.90	6.40	3.20	12.28	15.22	12.33	7.90
18443301	5.90	2.90	6.60	3.23	13.57	14.38	11.50	7.10
19761430	4.50	2.60	5.10	2.68	10.12	10.42	9.23	6.27
19761418	5.20	2.20	5.60	2.57	9.75	12.20	9.10	[6.20]
19761422	4.50	2.30	5.30	3.05	10.44	11.86	9.50	[5.72]
18561182	5.40	2.60	5.30	2.20	10.16	12.11	10.40	6.32
19761435	5.30	2.50	6.10	2.90	10.21	12.20	9.80	6.27
79112121	5.10	2.83	5.45	2.60	11.40	12.84	10.45	6.90
19861119	4.90	2.20	5.20	2.30	8.56	11.50	9.80	6.02
921153B	6.30	3.00	7.30	3.33	13.42	16.10	12.20	8.50
19761426	7.00	3.80	6.50	2.76	10.80	12.63	9.80	6.18
19761440	5.65	2.60	5.40	2.54	12.10	14.60	11.14	7.12
19761428	[6.60]	[3.35]	[7.00]	[3.10]	11.24	13.87	10.40	7.17
185231U	6.80	3.60	7.20	3.32	12.33	14.38	11.86	7.37
1948761	4.55	2.40	5.10	2.63	9.37	11.04	9.05	6.20
19861100	5.20	2.60	5.60	2.62	10.80	12.32	10.64	6.55
19861113	6.00	2.80	5.70	2.72	10.60	12.90	10.00	5.94

CAT	B20	B21	B22	B23	B24	V1	V2	V3
1948763U	10.10	4.78	7.80	.65	.55	7.85	10.60	6.85
19761427	7.90	4.30	6.74	.78	.62	7.20	9.40	7.80
19761415	7.80	4.29	6.48	.69	.85	7.60	10.20	6.60
19761431	11.00	5.24	8.32	.55	.75	7.75	11.20	6.50
18443301	9.70	5.34	8.59	1.00	1.30	8.25	10.20	6.90
19761430	8.20	3.91	6.30	.64	.63	7.30	9.00	6.40
19761418	8.20	3.94	6.33	.65	.98	7.10	9.70	5.90
19761422	8.60	3.86	6.54	.48	.69	7.50	9.70	6.60
18561182	7.00	4.20	6.20	.71	1.24	7.35	9.50	6.50
19761435	7.30	4.14	7.12	.61	1.00	7.40	10.35	7.20
79112121	8.20	4.44	6.62	.65	1.12	8.00	9.90	6.60
19861119	7.70	3.77	5.66	.60	.77	8.00	9.60	6.80
921153B	10.60	5.94	9.18	1.00	1.28	8.40	9.90	7.90
19761426	8.00	5.00	7.60	.85	.60	7.90	9.30	6.70
19761440	11.13	4.27	6.70	1.00	.37	7.60	8.75	7.70
19761428	9.00	5.47	[8.50]	1.00	.60	6.80	10.00	7.20
185231U	9.70	5.45	8.37	1.20	.55	8.00	9.85	9.00
1948761	8.00	3.70	6.12	.75	.32	6.28	8.86	7.10
19861100	7.80	3.83	6.17	.60	.90	7.00	9.69	6.80
19861113	7.70	4.20	6.77	.63	.56	7.90	9.50	8.00

PONGO

CAT	V4	V5	V6	V7	V8	V9	V10	V11
1948763U	6.55	7.45	7.09	6.80	5.78	9.38	5.10	2.00
19761427	7.26	6.00	5.76	6.50	5.72	9.01	5.67	.67
19761415	6.27	6.00	5.77	7.30	6.07	9.30	4.85	2.40
19761431	6.34	6.60	6.33	9.00	7.34	10.35	5.26	3.07
18443301	6.80	6.30	6.25	7.90	6.70	10.75	5.30	1.80
19761430	6.00	6.10	5.93	5.50	4.63	9.30	4.54	.88
19761418	5.70	6.70	6.45	[6.50]	[5.00]	9.35	4.63	2.33
19761422	6.32	6.30	5.86	[6.90]	[5.37]	9.85	5.14	2.56
18561182	6.24	6.60	6.19	6.90	5.97	9.20	5.02	1.65
19761435	6.60	6.10	5.90	6.60	5.67	9.55	5.30	2.26
79112121	6.39	5.80	5.60	7.10	5.75	9.60	5.44	2.47
19861119	6.25	5.80	5.60	6.90	5.54	8.70	5.14	2.00
921153B	7.64	6.90	6.56	8.20	7.12	10.60	5.55	1.30
19761426	6.68	6.50	6.16	6.50	5.22	9.05	5.20	1.74
19761440	7.20	6.10	6.00	8.00	5.60	9.35	5.57	1.70
19761428	6.75	7.20	6.87	[7.20]	[6.00]	[9.25]	4.95	2.13
185231U	8.20	6.20	6.00	8.40	6.20	10.90	5.84	2.20
1948761	6.70	5.90	5.65	7.20	6.05	8.45	5.14	2.57
19861100	6.36	6.20	5.86	7.30	6.30	9.50	4.95	2.24
19861113	7.55	6.50	6.20	6.20	5.00	9.10	5.77	1.20

CAT	V12	V13	V14	V15	V16	V17	V18	V19
1948763U	2.20	3.50	4.60	9.40	24.00	11.85	9.41	8.90
19761427	.70	5.30	6.00	8.42	22.70	10.90	8.68	8.53
19761415	2.60	4.27	4.80	7.68	21.50	10.15	8.49	8.20
19761431	3.20	5.49	5.80	9.99	26.50	12.52	9.84	9.48
18443301	2.50	5.81	6.00	10.58	28.30	11.90	9.20	9.25
19761430	1.00	4.05	4.50	7.10	18.00	9.45	7.72	7.20
19761418	2.40	[4.10]	[4.40]	7.37	21.00	9.90	8.21	8.15
19761422	2.80	[4.10]	[4.10]	7.37	20.00	9.90	8.10	7.38
18561182	1.70	4.74	5.30	6.80	19.50	9.90	8.10	7.82
19761435	2.30	3.90	4.30	7.64	20.50	9.80	8.20	8.01
79112121	2.60	4.14	4.50	8.21	22.70	10.20	8.18	7.76
19861119	2.10	4.30	4.80	7.26	18.50	9.15	7.70	7.52
921153B	1.40	6.30	6.80	10.63	27.00	12.40	9.95	10.05
19761426	1.80	4.20	4.70	8.40	22.50	11.05	8.80	8.92
19761440	2.80	4.58	5.20	10.50	29.50	12.60	8.29	8.26
19761428	2.40	4.65	4.80	9.24	25.00	11.25	9.10	9.24
185231U	3.30	5.14	5.10	10.90	29.00	12.50	10.25	9.60
1948761	3.10	4.16	4.10	6.74	18.70	9.30	7.75	7.62
19861100	2.30	4.70	4.00	8.13	20.10	10.37	8.47	7.84
19861113	1.20	4.40	5.00	8.03	22.00	11.50	8.92	8.55

PONGO

CAT	V20	V21	V22	V23	V24	F1	F2	F3
1948763U	9.90	13.30	13.00	1.25	1.67	9.31	1.81	3.75
19761427	8.20	12.55	11.32	1.40	1.45	7.76	.91	3.29
19761415	8.46	12.50	11.07	.85	1.12	8.01	1.20	3.60
19761431	10.31	13.40	13.85	1.50	1.76	9.21	1.84	3.63
18443301	9.90	12.70	13.10	1.10	1.63	8.80	1.50	3.45
19761430	6.84	11.60	10.69	1.00	2.15	7.55	1.14	3.32
19761418	8.30	12.30	11.04	1.32	1.54	7.34	1.38	3.00
19761422	7.42	12.10	10.84	1.30	1.20	7.14	1.03	3.20
18561182	7.81	12.10	11.08	1.32	1.10	7.90	1.05	3.50
19761435	7.77	12.50	11.27	.92	1.53	8.00	1.15	3.54
79112121	7.74	12.30	11.57	.53	1.12	7.67	1.24	[3.22]
19861119	7.27	12.00	10.59	.70	1.00	7.04	.95	3.32
921153B	11.14	14.10	14.80	.91	1.75	9.56	2.30	3.75
19761426	9.20	12.90	11.93	1.13	1.90	8.13	1.70	3.40
19761440	8.97	12.95	12.94	2.10	1.70	8.44	2.06	3.56
19761428	9.87	13.55	12.73	1.10	1.60	9.03	1.40	4.57
185231U	10.05	14.20	13.25	1.65	1.60	8.75	1.61	3.93
1948761	7.85	12.10	10.12	.90	1.13	7.53	1.25	3.20
19861100	7.97	12.00	11.53	.90	1.08	7.74	1.46	3.35
19861113	9.10	12.50	12.70	1.62	1.52	7.94	1.35	3.50

CAT	F4	F5	F6	F7	F8	F9	F10	F11
1948763U	4.35	.22	12.14	15.88	9.85	11.36	4.28	7.21
19761427	3.69	.51	9.48	13.35	8.23	10.07	3.23	6.00
19761415	3.78	.30	10.51	12.94	8.58	10.48	3.30	6.17
19761431	4.04	.30	12.06	16.70	9.90	11.37	3.65	6.97
18443301	3.63	.45	11.90	17.10	9.78	12.67	4.10	7.44
19761430	3.80	.30	9.83	12.60	8.00	10.10	3.50	6.05
19761418	3.65	.22	8.98	12.14	7.70	9.16	2.95	5.60
19761422	3.93	.22	9.65	12.07	7.54	9.34	2.90	5.66
18561182	3.90	.10	9.89	13.11	8.46	10.00	3.55	6.02
19761435	3.87	.35	9.65	12.61	8.48	10.18	3.40	6.23
79112121	3.42	.35	9.40	14.10	8.14	10.30	3.10	6.00
19861119	3.92	.28	9.13	11.93	7.48	9.13	2.65	5.38
921153B	4.30	.37	12.85	17.60	11.10	12.01	3.30	6.72
19761426	3.93	.15	10.28	14.14	8.56	9.80	4.20	6.87
19761440	4.05	.35	11.62	16.40	9.40	11.90	4.05	7.17
19761428	3.88	.40	11.47	16.70	9.70	11.45	4.60	7.17
185231U	4.40	.70	12.30	17.30	9.90	13.80	4.90	8.30
1948761	3.56	.20	10.10	13.01	7.80	9.55	2.93	5.34
19861100	3.74	.24	9.75	13.80	8.25	10.42	2.87	5.93
19861113	4.04	.24	10.90	15.17	9.07	10.56	4.00	6.68

PONGO

CAT	F12	F13	F14	F15	F16	F17	F18	F19
1948763U	9.79	7.47	3.17	.37	.54	9.97	5.43	5.62
19761427	7.70	5.43	2.17	.20	.91	9.73	5.76	5.76
19761415	7.98	6.18	2.56	.14	.52	9.28	5.08	5.31
19761431	10.34	8.12	3.44	.53	.71	10.90	6.04	6.30
18443301	9.07	7.16	3.45	.37	.76	11.51	6.57	6.61
19761430	9.57	6.93	2.80	.17	.97	8.98	5.06	4.81
19761418	8.74	6.70	3.00	.33	.80	8.92	4.83	4.61
19761422	8.33	6.51	3.04	.09	1.04	8.68	4.40	4.04
18561182	8.95	6.63	3.60	.25	.86	9.60	5.32	5.05
19761435	8.13	6.38	3.04	.11	.90	9.05	5.27	5.00
79112121	8.07	6.35	3.00	.	1.08	9.20	5.60	5.26
19861119	8.36	6.80	3.63	.00	1.00	8.60	4.66	4.51
921153B	12.38	8.34	3.76	.25	1.27	11.32	6.61	7.09
19761426	9.45	6.93	3.12	.54	1.00	9.70	5.76	5.67
19761440	9.88	8.15	3.50	.00	.70	10.50	6.10	5.80
19761428	11.50	8.50	2.90	.34	1.19	10.70	6.75	6.80
185231U	11.30	8.50	3.44	.24	1.17	11.67	7.00	6.44
1948761	6.35	5.05	2.60	.14	1.07	9.32	4.70	4.60
19861100	6.82	5.58	2.70	.25	.72	9.62	5.20	5.20
19861113	8.12	6.80	2.90	.18	1.00	10.39	5.70	5.35

CAT	F20	F21	F22	F23	F24	F25	F26	F27
1948763U	5.00	3.97	16.38	7.71	9.90	16.45	1.90	.82
19761427	4.30	2.87	14.10	7.82	9.80	14.50	1.74	.40
19761415	4.16	3.20	13.70	7.08	9.40	14.20	1.44	.33
19761431	5.63	3.87	17.05	7.93	10.60	17.20	1.77	.45
18443301	5.47	4.21	16.75	8.13	10.95	17.00	1.90	1.14
19761430	3.13	3.47	13.64	6.63	9.20	13.80	1.07	.43
19761418	3.62	2.98	14.03	7.16	9.40	14.10	1.12	.51
19761422	2.93	2.51	13.30	6.80	9.48	13.46	1.05	.40
18561182	3.55	3.07	14.05	7.20	9.00	14.10	1.33	.59
19761435	3.17	3.14	14.70	7.40	10.00	14.89	1.20	.50
79112121	3.50	2.95	13.15	7.38	9.80	13.80	1.20	.51
19861119	3.20	2.52	12.45	6.80	8.70	12.76	.95	.41
921153B	5.43	4.67	18.30	8.59	11.40	18.40	1.90	.90
19761426	5.87	3.45	16.00	7.96	9.60	16.40	1.97	.62
19761440	4.53	4.02	14.80	7.80	8.75	15.07	1.43	.87
19761428	5.70	3.84	[17.60]	8.20	[9.80]	[17.85]	1.67	.90
185231U	4.54	4.97	17.75	9.19	11.30	17.90	1.58	1.02
1948761	3.67	2.54	12.50	6.56	8.80	12.54	1.21	.45
19861100	3.70	2.15	13.00	6.90	9.10	13.20	1.17	.51
19861113	4.00	3.28	13.60	7.90	9.20	14.60	1.40	.67

A. AFARENSIS

CAT	M1	M2	M3	M4	M5	M6	M7	M8
LH4	[8.50]	4.38	.	.	[3.80]	.	2.24	[4.20]
LH13	.	.	.	.	.	.	2.46	.
AL145.35	.	[4.40]	.	.	[3.00]	.	[2.23]	.
AL188.1	.	.	.	.	.	.	2.31	.
AL198.1	[11.00]	[3.90]	.	.	[3.30]	.	1.90	[4.70]
AL207.13	[10.00]	[5.00]	.	.	3.55	.	2.86	[4.40]
AL266.1	.	4.36	.	.	2.75	.	2.47	[4.00]
AL277.1	.	[4.80]	.	.	3.90	.	2.07	.
AL288.1I	[7.00]	3.65	[8.80]	[2.75]	3.00	[5.70]	[2.20]	[3.80]
AL311.1	[9.60]	[4.50]	.	.	.	.	.	.
AL400.1	[8.25]	[4.50]	.	.	3.65	.	2.21	4.50
333W1AB	.	.	.	.	.	.	2.62	.
333W.12	.	[4.00]	.	.	2.90	.	[2.15]	.
333W.58	.	.	.	.	[3.50]	.	.	.
333W.60	[11.40]	[5.00]	.	.	4.20	.	[2.74]	3.00
RECONSTR	10.45	5.38	14.05	5.54	4.13	[9.13]	2.87	3.80

CAT	M9	M10	M11	M12	P1	P2	P3	P4
LH4	[6.60]	3.00	[3.00]	[7.30]	.	.	.	.
AL145.35	.	2.70	.	[6.50]	.	.	.	.
AL188.1	.	3.20	3.30	6.75	.	.	.	.
AL198.1	[7.60]	3.10	2.85	[5.50]	.	.	.	.
AL199.1	.	.	.	.	[5.20]	[3.00]	6.10	[6.20]
AL200.1	.	.	.	.	[6.80]	3.50	7.10	6.72
AL207.13	[8.00]	3.00	2.65	[6.80]	.	.	.	.
AL266.1	[6.20]	3.00	2.25	[7.00]	.	.	.	.
AL277.1	.	3.65	.	[6.30]	.	.	.	.
AL288.1I	[6.40]	2.95	[2.40]	[5.50]	.	.	.	.
AL311.1	.	.	.	[6.00]	.	.	.	.
AL400.1	6.40	[3.40]	.	6.90	.	.	.	.
333W1AB	.	3.50	3.00	.	.	.	.	.
333W.12	.	3.05	.	[6.00]	.	.	.	.
333W.60	[8.60]	3.80	[3.35]	7.00	.	.	.	.
RECONSTR	6.36	4.00	3.50	7.67	7.12	3.50	7.50	6.65

CAT	P5	P6	P7	P8	P9	B1	B2	B3
AL199.1	[5.60]	[5.80]	1.05	.	2.36	.	.	.
AL200.1	7.50	6.33	.75	1.10	3.13	.	.	.
AL333.2	.	.	.85	.	[2.10]	.	.	.
333.45AB	.	.	.	.	.	[2.90]	.	[12.60]
RECONSTR	7.60	6.34	.83	1.12	2.94	3.76	2.90	11.48

A. AFARENSIS

CAT	B4	B5	B6	B7	B8	B9	B10	B11
333.45AB	[8.00]	[6.80]	[5.60]	[3.00]	[4.60]	.	3.15	3.00
RECONSTR	7.50	7.92	6.94	[4.20]	[5.52]	[7.30]	2.24	2.28

CAT	B12	B13	B14	B15	B16	B17	B18	B19
AL162.28	.	.	.	.	7.90	.	.	.
333.45AB	.	3.00	.	.	[9.70]	[12.70]	[10.00]	4.80
RECONSTR	4.00	2.10	3.60	.	9.27	[13.10]	10.26	[6.00]

CAT	B20	B21	B22	B23	B24	V1	V2	V3
AL162.28	5.70	.	.	.	.	.	[8.60]	.
AL166.9	.	.	.	.15	.50	.	.	.
333.45AB	5.40	.	.	.30	.70	.	[9.70]	.
RECONSTR	6.30	.	5.50	.	.	7.85	10.40	.

CAT	V4	V5	V6	V7	V8	V9	V10	V11
AL162.28	.	.	.	.	.	.	.	3.20
333.45AB	.	.	.	7.30	6.10	.	.	3.25
RECONSTR	.	.	.	7.40	6.18	[9.35]	.	3.38

CAT	V12	V13	V14	V15	V16	V17	V18	V19
AL162.28	3.40	.	.	.	.	.	.	.
333.45AB	3.30	3.92	4.00	.	.	[12.00]	.	.
RECONSTR	3.50	3.77	4.00	9.52	.	12.44	10.16	9.82

CAT	V20	V21	V22	V23	V24	F1	F2	F3
333.45AB	.	.	.	2.67	3.45	.	.	.
AL333.84	.	.	.	[2.00]	2.15	.	.	.
RECONSTR	10.35	15.00	13.14	2.74	2.95	9.01	3.74	3.30

CAT	F4	F5	F6	F7	F8	F9	F10	F11
RECONSTR	3.57	1.20	13.25	13.53	9.87	[9.88]	2.30	5.40

CAT	F12	F13	F14	F15	F16	F17	F18	F19
AL200.1	.	.	2.08	.	.91	.	.	.
RECONSTR	7.11	5.50	2.10	.	1.72	.	.	.

CAT	F20	F21	F22	F23	F24	F25	F26	F27
RECONSTR	.	2.67	12.80	8.62	9.40	13.04	.	.

A. AFRICANUS

CAT	M1	M2	M3	M4	M5	M6	M7	M8
MLD18	[8.60]	[5.00]	.	.	.	.	2.95	[3.90]
MLD19	.	.	.	.	.	.	2.40	.
MLD22	.	.	.	.	.	.	2.50	.
MLD29	.	.	.	.	.	.	[2.28]	.
MLD34	.	.	.	.	.	.	2.60	.
MLD40	[9.00]	[5.80]	[12.00]	4.42	[3.35]	6.65	3.05	.
STW14	.	.	.	.	.	.	2.32	.
STW109	.	.	.	.	.	.	2.63	.
STW384	.	.	.	.	.	.	[2.10]	.
STW404	.	[4.60]	.	.	.	.	[2.40]	.
STS7	.	[4.00]	.	.	4.20	.	[2.40]	.
STS36	[9.20]	[4.50]	11.60	5.24	3.20	6.86	2.62	5.75
STS52	[9.00]	.	[10.70]	4.58	3.10	[7.50]	2.62	5.77

CAT	M9	M10	M11	M12	P1	P2	P3	P4
MLD6	.	.	.	.	.	[2.60]	.	[5.30]
MLD9	.	.	.	.	.	[4.00]	.	[6.80]
MLD18	[6.60]	3.45	2.90	6.60	.	.	.	.
MLD19	.	.	2.60	.	.	.	.	.
MLD29	.	[3.20]	.	.	.	.	.	.
MLD34	.	3.20	.	.	.	.	.	.
MLD40	.	3.50	3.10	[6.80]	.	.	.	.
STW13	.	.	.	.	6.58	.	.	.
STW14	.	3.10	2.75	.	.	.	.	.
STW73	.	.	.	.	5.50	3.15	[6.40]	5.60
STW404	.	2.60	.	[6.50]	.	.	.	.
STS5	.	.	.	.	6.55	3.60	7.23	6.80
STS7	.	3.60	3.15	[7.30]	.	.	.	.
STS36	7.50	3.50	3.00	6.90	.	.	.	.
STS52	7.93	2.80	2.50	6.40	[5.60]	2.60	6.90	6.10
STS53	.	.	.	.	5.30	3.67	6.44	6.38
STS71	.	.	.	.	.	.	[7.30]	.
TM1511	.	.	.	.	[6.00]	.	.	.

CAT	P5	P6	P7	P8	P9	B1	B2	B3
MLD6	.	[5.20]	1.15	.	[2.00]	.	.	.
MLD9	.	[6.90]	1.35	.	[2.80]	.	.	.
MLD37.38	.	.	.	.	.	2.80	2.74	9.70
STW13	[7.00]	.	[1.50]	.	3.25	.	.	.
STW73	.	.	1.10	1.65	2.85	.	.	.
STW252AO	.	.	[1.50]	.	[2.80]	.	.	.
STW391	.	.	[.70]	.	.	.	.	.
STS5	.	.	1.60	1.35	2.96	3.00	2.40	9.20
STS17	[6.50]	.	1.50	.	2.70	.	.	.
STS19	.	.	.	.	.	2.70	2.10	9.15
STS25	.	.	.	.	.	.	.	[9.00]
STS26	.	.	.	.	.	2.72	2.11	.
STS52	7.12	5.56	1.60	.	2.74	.	.	.
STS53	[6.20]	6.26	.90	.65	2.83	.	.	.
STS71	.	.	.60	.	2.94	.	.	.
TM1511	.	.	1.50	[1.30]	[3.20]	.	.	.
TM3009	.	.	.	.	[2.40]	.	.	.

A. AFRICANUS

CAT	B4	B5	B6	B7	B8	B9	B10	B11
MLD37.38	6.85	6.20	4.70	2.35	4.65	[4.80]	2.50	2.40
STS5	6.90	6.60	4.77	2.70	4.70	5.10	2.30	2.40
STS19	6.70	6.27	5.00	2.48	4.36	[5.00]	2.30	2.10
STS25	.	.	4.15	[1.20]	[4.00]	[4.60]	2.40	2.60

CAT	B12	B13	B14	B15	B16	B17	B18	B19
MLD1	.	.	.	.	.	10.30	.	.
MLD37.38	4.60	2.30	4.70	2.20	7.90	11.76	8.50	5.10
STS5	5.40	2.90	5.10	2.50	7.20	[11.30]	9.10	5.50
STS19	4.15	2.30	4.05	2.02	.	.	[8.50]	.
STS25	5.10	3.60	4.10	.	[7.60]	.	.	.

CAT	B20	B21	B22	B23	B24	V1	V2	V3
MLD37.38	6.50	3.70	5.22	.65	.70	.	9.90	.
STW252AO	.	.	.	.	.	.	[8.40]	.
STS5	5.80	3.50	5.53	.40	.65	8.50	9.70	8.80
STS19	.	[4.40]	[5.37]	.70	1.05	.	.	.
STS25	.	.	.	.	[.50]	.	.	.
STS71	.	.	.	.60	.	[6.60]	.	8.60

CAT	V4	V5	V6	V7	V8	V9	V10	V11
MLD1	.	.	.	7.70	6.62	.	.	4.55
MLD3	.	8.20	7.50	.	.	.	.	.
MLD37.38	.	8.50	7.69	7.00	5.69	9.25	.	4.07
STW252AO	.	8.20	7.42	.	.	.	.	.
STS5	7.50	9.10	8.30	7.20	5.90	10.30	6.90	4.65
STS25	.	8.50	8.06	.	.	.	.	.

CAT	V12	V13	V14	V15	V16	V17	V18	V19
MLD1	5.10	3.24	3.30	.	.	.	.	.
MLD37.38	4.50	2.54	2.50	.	.	10.20	.	.
STS5	5.60	1.64	1.60	[8.10]	23.00	9.50	9.00	8.80
STS25	.	.	.	.	.	[8.40]	.	.
STS26	.	.90	1.00	.	.	.	.	.
STS71	5.90	1.76	1.70	7.85	23.50	[8.00]	7.76	7.55

A. AFRICANUS

CAT	V20	V21	V22	V23	V24	F1	F2	F3
MLD6	.	.	.	.	.	.	1.60	.
MLD37.38	.	.	10.80	1.95	1.80	.	.	.
STW13	.	.	.	.	.	.	2.03	.
STS5	8.24	14.40	10.70	2.18	1.80	8.30	1.70	3.55
STS17	.	.	.	.	.	[7.00]	[1.80]	2.47
STS25	.	.	[9.20]	.	.	.	.	.
STS52	.	.	.	.	.	[8.40]	1.84	.
STS63	.	.	.	.	.	.	.	3.30
STS71	7.44	12.40	[9.70]	2.30	2.00	[8.00]	1.65	3.40

CAT	F4	F5	F6	F7	F8	F9	F10	F11
STW252AO	.	.60	.	.	.	.	.	.
STS5	2.94	.90	11.04	12.60	9.27	10.60	1.85	6.00
STS52	.	.	[10.10]	.	.	[9.10]	2.25	5.00
STS63	3.05	.	.	.	.	.	.	.
STS71	3.10	.70	[10.20]	[11.20]	[8.30]	[9.40]	1.50	4.93

CAT	F12	F13	F14	F15	F16	F17	F18	F19
MLD6	.	4.57	[2.50]	.22	[.93]	.	.	.
MLD9	.	.	[3.90]	.	.93	.	.	.
STW13	7.70	5.70	2.62	.60	1.27	.	.	.
STW252AO	.	.	[2.60]	.	.	.	.	.
STW391	.	.	[2.90]	.	.	.	.	.
STS5	6.64	4.90	2.67	.15	1.70	[10.30]	4.55	5.20
STS17	[6.50]	[5.00]	2.70	.	.63	.	.	.
STS52	6.85	4.96	2.51	.42	.82	[9.00]	.	.
STS53	.	.	2.25	.	.84	.	.	.
STS63	.	7.17	.	.	.	.	.	.
STS71	7.10	5.34	[2.78]	.	.87	[8.80]	4.30	4.84

STW13	.	3.20	.	.	.	.	.	.
STS5	3.64	2.60	12.40	8.35	9.80	12.40	.67	.34
STS17	.	[2.30]	.	.	.	.	.	.
STS52	.	2.43	.	.	.	.	.	.
STS71	3.70	2.80	.	7.10	.	.	[.80]	[.46]

A. ROBUSTUS

CAT	M1	M2	M3	M4	M5	M6	M7	M8
SK23	.	.	13.10	5.35	4.25	9.12	2.92	.
SK34	.	.	[13.50]	5.55	.	10.50	3.25	.
SK844	.	.	.	[4.65]	.	.	.	.
SK858	.	.	.	4.80	.	.	.	.
TM1517AB	.	.	.	.	.	.	2.92	.

CAT	M9	M10	M11	M12	P1	P2	P3	P4
SK11	.	.	.	.	[5.50]	.	.	.
SK12AB	8.47	4.20	3.40	6.40	.	.	.	.
SK23	.	3.60	3.20	7.70	.	.	.	.
SK34	.	3.75	3.55	[7.80]	.	.	.	.
SK46	.	.	.	.	.	[3.85]	7.29	7.15
SK48	.	.	.	.	5.70	3.85	6.84	6.80
SK79	.	.	.	.	[5.25]	3.67	6.80	7.30
SK83AB	.	.	.	.	6.84	4.50	7.74	7.96
SK844	.	.	3.40	.	.	.	.	.
SK876	.	[4.30]	4.95	.	.	.	.	.
TM1517AB	.	3.45	3.00	.	6.50	.	[7.57]	.

CAT	P5	P6	P7	P8	P9	B1	B2	B3
SK11	.	6.84	1.54	.	2.18	.	.	.
SK12AB	.	.	1.40	.	2.25	.	.	.
SK46	[6.20]	7.03	1.30	1.55	2.47	.	.	.
SK48	[6.50]	6.55	1.50	[2.20]	[2.88]	.	.	.
SK65	.	.	1.25	.	[2.20]	.	.	.
SK79	[6.17]	7.04	1.50	1.70	2.60	.	.	.
SK83AB	6.64	7.94	1.45	1.80	3.05	2.64	2.42	.

CAT	B4	B5	B6	B7	B8	B9	B10	B11
TM1517AB	[6.70]	[6.60]	[4.80]	[1.90]	[4.20]	[6.10]	3.40	2.20

CAT	B12	B13	B14	B15	B16	B17	B18	B19
SK48	.	.	.	2.30	.	.	.	.
TM1517AB	6.20	3.40	5.75	.	.	[12.80]	[11.00]	.

A. ROBUSTUS

CAT	B20	B21	B22	B23	B24	V1	V2	V3
SK46	.	.	.	.50	.80	.	.	.
SK48	.	3.30	3.67	.40	.40	8.23	.	6.30
SK83AB	.	.	.	.60	1.20	.	.	.
TM1517AB	.	3.86	[5.50]	.63	.55	.	.	.

CAT	V4	V5	V6	V7	V8	V9	V10	V11
SK46	.	.	.	.	.	.	2.22	.
SK48	6.03	.	.	.	.	.	3.68	.

CAT	V12	V13	V14	V15	V16	V17	V18	V19
SK48	.	.	.	.	.	11.10	9.25	9.00
TM1517AB	.	.	.	.	.	[10.80]	.	9.25

CAT	V20	V21	V22	V23	V24	F1	F2	F3
SK46	.	.	.	2.40	2.54	.	.	.
SK48	9.46	[13.50]	12.10	.	.	10.10	[2.50]	3.60
SK83AB	.	.	.	3.00	2.64	.	.	.
TM1517AB	[10.30]	.	11.00	.	.	.	.	.

CAT	F4	F5	F6	F7	F8	F9	F10	F11
SK12AB	.	.	.	.	.	[11.50]	.40	[6.00]
SK46	.	.	.	.	.	[10.70]	1.10	5.40
SK48	3.00	1.25	12.10	[15.00]	[9.80]	10.45	.50	5.10
TM1517AB	.	.	[11.70]	[12.70]	.	.	.	.

CAT	F12	F13	F14	F15	F16	F17	F18	F19
SKW12	.	.	.	.	1.00	.	.	.
SK11	.	.	2.83	.	.	.	.	.
SK12AB	.	4.47	2.60	.	1.21	.	.	.
SK46	.	.	[2.40]	.	1.13	[10.70]	.	.
SK48	7.64	5.65	3.14	.43	1.20	9.90	4.96	5.88
SK79	.	.	3.07	.	1.25	.	.	.
SK83AB	6.74	5.10	[2.52]	[.40]	1.32	.	.	.
TM1517AB	.	.	.	.	1.07	.	4.40	5.58

CAT	F20	F21	F22	F23	F24	F25	F26	F27
SK46	.	2.60	.	.	.	.	.	.
SK48	5.25	3.38	9.80	8.30	7.80	9.85	1.63	.50
SK83AB	.	3.50	12.60	.	8.65	12.30	.	.
TM1517AB	[5.25]	3.20	.	8.30	.	.	1.20	.76

A. BOISEI

CAT	M1	M2	M3	M4	M5	M6	M7	M8
ER403	.	.	.	.	.	.	3.50	.
ER404	.	.	.	.	.	.	3.55	.
ER725	.	.	.	.	.	.	3.57	.
ER726	.	.	.	.	.	.	3.35	.
ER728	.	.	.	.	.	.	2.65	.
ER729	[13.12]	5.52	[14.50]	5.68	4.95	[10.50]	3.40	6.43
ER733	.	.	.	.	.	.	2.93	.
ER801	.	.	.	.	.	.	3.16	.
ER805	.	.	.	.	.	.	3.55	.
ER810	.	.	.	.	.	.	3.50	.
ER818	.	.	.	.	[5.20]	.	3.97	.
ER1468	.	.	.	.	.	.	3.37	.
ER1469	.	.	.	.	.	.	4.03	.
ER1806	.	.	.	.	.	.	3.56	.
ER3230	[10.50]	[4.80]	.	.	4.50	.	3.85	6.90
ER3729	.	.	.	.	.	.	2.77	.
ER3889	.	.	.	.	[4.30]	.	.	.
PENINJ	10.80	5.85	12.90	5.30	4.60	7.55	3.46	5.50

CAT	M9	M10	M11	M12	P1	P2	P3	P4
ER403	.	4.40	4.30	7.80	.	.	.	.
ER404	.	4.20	4.55	8.50	.	.	.	.
ER405	.	.	.	.	[6.64]	[4.06]	[8.24]	[8.13]
ER406	.	.	.	.	6.73	[3.60]	7.60	7.98
ER725	.	3.90	3.25	[7.50]	.	.	.	.
ER726	.	4.20	3.90	7.50	.	.	.	.
ER727	.	3.40	.	.	.	.	.	.
ER728	.	3.55	3.30	.	.	.	.	.
ER729	9.00	4.60	4.45	8.01	.	.	.	.
ER733	.	3.70	.	.	.	.	.	.
ER801	.	4.15	3.95	[7.50]	.	.	.	.
ER805	.	3.85	3.30	.	.	.	.	.
ER810	.	3.95	4.05	[8.00]	.	.	.	.
ER818	.	4.90	4.50	9.40	.	.	.	.
ER819	.	3.50	.	.	.	.	.	.
ER1468	.	4.70	4.50	.	.	.	.	.
ER1469	.	4.40	4.00	[7.50]	.	.	.	.
ER1806	.	4.18	[3.10]	.	.	.	.	.
ER2602	.	4.00	4.00	[7.50]	.	.	.	.
ER3230	[9.50]	3.90	[3.50]	[8.75]	.	.	.	.
ER3729	.	3.70	3.50	[8.00]	.	.	.	.
ER3889	.	[3.95]	.	.	.	.	.	.
OH5	.	.	.	.	7.78	3.84	8.30	7.83
PENINJ	7.82	3.90	3.30	7.60	.	.	.	.

A. BOISEI

CAT	P5	P6	P7	P8	P9	B1	B2	B3
ER405	[6.94]	[8.34]	1.75	2.17	[2.57]	.	.	.
ER406	.	.	1.83	1.60	[2.13]	2.90	3.22	13.20
ER407	.	.	.	.	.	2.92	2.88	10.20
ER732	.	.	.	.	.	.	.	[10.70]
ER1478	.	.	[1.77]	.	.	.	.	.
ER3891	6.50	.	1.27	.	2.62	.	.	.
OH5	8.00	7.67	1.96	1.53	3.13	2.80	2.60	12.22

CAT	B4	B5	B6	B7	B8	B9	B10	B11
ER406	8.50	7.90	6.45	[2.00]	5.77	6.06	3.65	2.90
ER407	7.30	6.47	5.30	2.84	4.40	6.10	2.55	2.34
ER732	.	.	[3.50]	[1.40]	[4.20]	[6.10]	3.34	[1.75]
OH5	8.10	7.25	5.96	2.86	5.75	[6.50]	3.50	2.35

CAT	B12	B13	B14	B15	B16	B17	B18	B19
ER406	5.50	3.35	5.20	3.00	9.97	13.17	11.86	5.47
ER407	4.72	3.50	3.95	2.28	8.16	9.70	11.70	4.54
ER732	4.90	[3.00]	.	.	.	[11.00]	[7.80]	.
OH5	6.00	3.10	5.50	2.70	9.14	[13.20]	[13.60]	5.27

CAT	B20	B21	B22	B23	B24	V1	V2	V3
ER406	7.10	4.01	6.13	1.35	1.25	8.00	9.10	10.20
ER407	5.00	.	.	.	.	8.32	9.70	.
ER732	.	.	.	1.12	.45	[8.33]	[8.80]	6.90
ER3891	.	.	.	.40	.85	.	.	.
OH5	6.70	4.10	5.92	.90	.90	[8.65]	10.40	10.30

CAT	V4	V5	V6	V7	V8	V9	V10	V11
ER406	9.16	9.30	8.63	7.20	6.22	10.65	5.80	3.96
ER407	.	10.50	9.40	7.40	6.05	.	.	4.02
ER732	6.10	.	.	.	.	.	3.45	.
ER2602	.	.	.	.	.	.	.	3.60
OH5	9.50	9.80	8.90	7.90	5.78	9.35	6.50	3.67

H. ERECTUS

CAT	M1	M2	M3	M4	M5	M6	M7	M8
ER730	.	5.09	.	.	3.10	.	2.00	[5.60]
ER731	.	.	.	.	[2.74]	.	.	.
ER817	.	.	.	.	[2.67]	.	.	.
ER992	[10.00]	.	[13.00]	5.05	3.56	7.90	2.30	.
ER1501	.	.	.	.	[2.90]	.	[1.83]	.
ER1506	.	.	.	.	.	.	2.39	.
ER3950	.	.	.	.	3.10	.	.	.
OH22	[10.00]	[5.00]	[11.00]	.	[3.30]	.	2.35	[4.60]
LH29	.	.	.	.	.	.	2.38	.
BK67	[8.50]	4.55	12.10	5.38	3.10	.	2.34	4.10
BL8518	[10.00]	3.91	.	.	2.80	7.47	2.21	[4.80]
SK15	.	[4.20]	[12.00]	.	2.65	.	2.60	.
MAUR	10.55	5.80	12.30	5.22	3.55	7.15	2.30	5.73
HI	8.80	4.59	10.70	4.10	3.26	6.95	1.76	[4.26]
GI	9.92	.	11.00	4.13	3.80	7.65	1.90	5.80

CAT	M9	M10	M11	M12	P1	P2	P3	P4
ER730	[7.20]	3.05	2.90	[5.30]	.	.	.	.
ER731	.	2.32	.	.	.	.	.	.
ER817	.	2.70	.	.	.	.	.	.
ER992	.	3.00	3.20	[6.00]	.	.	.	.
ER1501	.	2.60	2.50	[6.00]	.	.	.	.
ER1506	.	3.05	.	.	.	.	.	.
ER3733	.	.	.	.	[4.80]	.	6.40	.
OH22	[7.60]	2.65	3.00	5.90	.	.	.	.
OH23	.	3.00	.	.	.	.	.	.
OH51	.	3.40	.	.	.	.	.	.
LH29	.	.	3.60	.	.	.	.	.
BK67	6.33	3.20	3.15	5.84	.	.	.	.
BL8518	6.95	2.75	3.00	6.20	.	.	.	.
SK15	.	2.70	2.35	[6.00]	.	.	.	.
SAN17	.	.	.	.	5.00	4.80	7.20	8.07
MAUR	7.30	3.50	3.05	5.98	.	.	.	.
HI	6.50	2.65	2.80	[5.40]	.	.	.	.
GI	7.48	3.55	3.25	6.68	.	.	.	.

CAT	P5	P6	P7	P8	P9	B1	B2	B3
ER807	.	.	.	1.96	.	.	.	.
ER3733	[5.80]	.	1.50	[1.35]	3.30	3.50	3.20	12.00
ER3883	.	.	.	.	.	3.13	2.60	11.51
OH9	.	.	.	.	.	.	.	12.40
OH12	.	.	[.65]	.	.	.	.	.
SAN17	.	7.35	1.50	[.75]	3.35	4.03	3.15	12.46
SKULLI	.	.	.	.	.	.	.	[13.26]
SKULL II	.	.	.	.	.	.	.	[11.90]
SKULLIII	.	.	.	.	.	.	.	[12.90]
PITH II	.	.	.	.	.	.	.	11.55
SKULL3	.	.	.	.	.	.	.	12.30

H. ERECTUS

CAT	B4	B5	B6	B7	B8	B9	B10	B11
ER3733	8.85	7.85	5.72	3.55	6.05	6.50	3.02	2.45
ER3883	8.40	7.80	5.75	3.10	5.35	[6.85]	2.90	2.50
OH9	9.20	8.30	6.73	3.10	5.78	7.85	2.63	2.75
SAN17	[9.73]	[9.20]	[6.20]	5.40	5.95	[9.35]	2.80	2.26

CAT	B12	B13	B14	B15	B16	B17	B18	B19
ER730	.	.	.	.	10.97	.	.	.
ER3733	5.40	3.10	5.60	2.60	11.80	13.05	[11.70]	7.74
ER3883	5.60	2.90	5.30	2.41	10.80	13.80	10.30	5.70
OH9	6.00	2.98	[6.00]	[3.10]	12.20	14.25	.	6.60
OH12	.	.	.	.	[9.80]	.	.	.
SAN17	5.90	2.40	[5.30]	[2.77]	[10.50]	15.80	11.40	6.84
SKULLI	.	.	.	.	11.66	13.70	[11.40]	[5.38]
SKULL II	.	.	.	.	11.33	14.74	9.50	6.27
SKULLIII	.	.	.	.	11.66	[14.30]	.	6.10
PITH II	.	.	.	.	11.20	14.05	11.00	6.20
SKULL3	.	.	.	.	11.64	14.50	11.20	6.70

CAT	B20	B21	B22	B23	B24	V1	V2	V3
ER3733	9.50	[4.62]	[6.50]	.80	.35	10.75	13.10	11.40
ER3883	6.00	.	.	.85	.55	9.40	12.50	[12.00]
OH9	8.30	.	.	1.90	.60	[10.60]	[13.20]	12.00
OH12	[5.00]	.	.	.	.	.	.	.
SAN17	10.00	.	.	.	.	11.20	14.10	13.00
SKULLI	11.00	.	.	.	.	10.70	13.50	13.30
SKULL II	11.00	.	.	.	.	10.50	13.65	[13.00]
SKULLIII	9.60	.	.	.	.	10.58	13.80	13.20
PITH I	.	.	.	.	.	9.45	12.90	[12.40]
PITH II	9.50	.	.	.	.	10.94	13.45	.
SKULL3	9.00	.	.	.	.	10.10	13.30	[13.50]

CAT	V4	V5	V6	V7	V8	V9	V10	V11
ER730	.	.	.	8.60	6.34	.	.	4.79
ER3733	10.27	8.80	7.85	12.00	8.80	[10.80]	7.04	6.80
ER3883	[10.00]	[9.50]	[8.25]	10.90	7.45	10.20	7.47	6.50
ER3892	.	.	.	.	.	.	6.30	.
OH9	10.37	11.20	11.13	11.70	7.71	10.60	7.17	5.44
OH12	.	.	.	.	.	.	.	[5.00]
SAN17	10.65	[14.50]	[13.00]	[10.00]	[7.18]	10.85	8.50	3.57
SKULLI	11.33	11.80	11.10	[13.40]	[8.83]	[11.60]	9.22	5.07
SKULL II	[10.42]	9.60	9.20	11.80	8.70	[11.00]	8.88	4.73
SKULLIII	11.67	9.00	8.74	12.00	8.38	[11.10]	9.34	6.15
PITH I	[10.46]	10.00	9.36	.	.	.	8.10	3.65
PITH II	[8.20]	10.10	9.60	[10.70]	[8.00]	.	.	4.60
SKULL3	[11.00]	9.80	9.20	10.70	7.86	11.00	8.54	4.60

H. ERECTUS

CAT	V12	V13	V14	V15	V16	V17	V18	V19
ER730	5.20	2.96	3.40	.	.	.	.	.
ER3733	7.30	4.75	7.80	9.00	23.00	12.45	10.15	8.25
ER3883	8.20	2.74	2.80	8.35	24.50	11.80	10.70	9.30
OH9	6.50	5.18	5.20	8.60	28.00	13.00	10.55	.
OH12	[5.70]	.	.	.	.	.	.	.
SAN17	4.00	5.48	5.60	.	.	13.70	10.90	9.30
SKULLI	5.20	7.05	8.20	.	.	[13.40]	.	.
SKULL II	4.90	6.47	6.90	.	.	12.60	.	.
SKULLIII	6.30	5.50	5.70	.	.	[13.40]	.	.
PITH I	3.75	.	.	.	.	.	.	.
PITH II	4.60	5.50	6.20	.	.	11.80	.	.
SKULL3	4.70	5.50	6.00	.	.	12.53	.	.

CAT	V20	V21	V22	V23	V24	F1	F2	F3
ER3733	7.60	17.75	13.00	1.65	1.80	[10.60]	2.12	4.70
ER3883	7.75	17.40	12.80	3.10	2.55	10.89	2.36	4.44
OH9	.	19.60	13.65	.	2.60	.	2.80	.
OH12	.	.	.	[1.80]	1.74	.	.	.
SAN17	9.00	19.60	14.50	.	.	10.80	2.82	4.50
SKULLI	.	19.30	[12.20]	.	.	.	.	.
SKULL II	.	17.90	.	1.90	1.29	.	.	.
SKULLIII	.	19.15	.	.	.	.	.	.
PITH I	.	[17.40]	.	.	.	.	.	.
PITH II	.	[16.50]	12.60	.	.	.	.	.
SKULL3	.	[18.25]	13.80	1.75	1.92	.	.	.

CAT	F4	F5	F6	F7	F8	F9	F10	F11
ER3733	3.62	1.20	12.35	13.50	[10.95]	9.90	2.10	5.72
ER3883	3.56	1.08	12.13	14.00	11.05	.	.	.
OH9	.	1.95	.	.	12.60	.	.	.
SAN17	3.68	1.00	12.65	13.90	10.90	11.86	2.45	6.50

CAT	F12	F13	F14	F15	F16	F17	F18	F19
ER3733	7.92	5.32	3.63	.71	[1.00]	9.70	4.41	4.70
ER3883	.	5.66	[3.10]	.65	.	.	.	.
OH9	.	.	.	1.05	.	.	.	.
SAN17	7.10	5.00	2.96	.	.	11.34	.	.

CAT	F20	F21	F22	F23	F24	F25	F26	F27
ER3733	3.60	3.29	11.75	7.68	10.20	11.75	1.15	.40
ER3883	.	.	.	8.30	10.25	.	.	.
OH9	.	.	.	9.04	11.50	.	.	.
SAN17	.	3.62	13.20	8.22	10.80	12.84	.	.

APPENDIX 4A: CORRELATION AND ROTATED FACTOR MATRICES

TABLE 4.01: MANDIBLE: CORRELATION MATRIX

	M2	M5	M7	M8	M9	M10	M11	M12
M2	1.00000							
M5	.28390	1.00000						
M7	.43381	.45078	1.00000					
M8	.34077	.12092	.35907	1.00000				
M9	.39384	.08192	.60510	.62863	1.00000			
M10	.33093	.88036	.67206	.16139	.14654	1.00000		
M11	.28103	.81286	.41028	.12263	-.01702	.84914	1.00000	
M12	.12267	.77685	.29672	-.04560	-.18949	.69638	.78005	1.00000

TABLE 4.02: MANDIBLE: ROTATED PC MATRIX

	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
M11	.92618	.05243	.06445	.13115
M5	.91321	.16567	.05376	.10364
M12	.91115	-.06540	-.08114	-.00289
M10	.87551	.38604	.01059	.12209
M7	.36775	.86641	.12050	.18174
M9	-.13949	.72394	.55803	.17995
M8	.05251	.18624	.95603	.13641
M2	.15545	.20814	.17010	.94997

TABLE 4.03: PALATE: CORRELATION MATRIX

	P1	P2	P3	P4	P7	P9
P1	1.00000					
P2	.56270	1.00000				
P3	.97207	.59943	1.00000			
P4	.30612	.81567	.37722	1.00000		
P7	.56869	.47915	.62924	.44449	1.00000	
P9	.82447	.64867	.82464	.35683	.51796	1.00000

TABLE 4.04: PALATE: ROTATED PC MATRIX

	FACTOR 1	FACTOR 2	FACTOR 3
P1	.92837	.15196	.25619
P3	.89502	.21116	.32282
P9	.87907	.28323	.13186
P4	.09045	.94506	.22121
P2	.44864	.85076	.11222
P7	.34239	.24560	.90115

TABLE 4.05: BASE: CORRELATION MATRIX

	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13
B3	1.00000										
B4	.76688	1.00000									
B5	.37680	.74525	1.00000								
B6	.39864	.57742	.81264	1.00000							
B7	.51101	.69019	.65823	.58901	1.00000						
B8	.62036	.74797	.58158	.48548	.67760	1.00000					
B9	.37787	.65329	.79729	.66626	.67631	.48123	1.00000				
B10	.85465	.46918	-.05645	-.08325	.24532	.46592	-.01477	1.00000			
B11	.70688	.47419	.11253	.26644	.24711	.35488	.04676	.61141	1.00000		
B12	.78081	.53664	.20745	.16142	.30334	.40033	.15366	.74568	.68579	1.00000	
B13	.62019	.35370	-.01590	-.09340	.03312	.19180	-.15341	.73744	.66672	.79266	1.00000

TABLE 4.06: BASE: ROTATED PC MATRIX

	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
B13	.93643	-.08421	-.06269	.05220
B12	.90973	.18634	.09191	.05057
B10	.83975	-.14515	.46509	-.05386
B3	.77433	.32321	.43052	.14659
B11	.71192	.04878	.15397	.62383
B5	.03079	.94458	.15032	.06978
B9	-.00951	.89787	.20094	-.14061
B6	-.04239	.81599	.12859	.48851
B4	.46255	.68161	.43714	.04448
B7	.10038	.63331	.60673	.03901
B8	.23855	.41710	.79252	.11054

TABLE 4.07: VAULT: CORRELATION MATRIX

	V1	V3	V4	V5	V6	V10	V11	V12
V1	1.00000							
V3	.66763	1.00000						
V4	.62755	.96248	1.00000					
V5	.61736	.47207	.38891	1.00000				
V6	.62926	.50785	.41958	.98060	1.00000			
V10	.73749	.82886	.83431	.55327	.56152	1.00000		
V11	.44289	.43962	.43281	.25212	.21382	.44846	1.00000	
V12	.29988	.42018	.40788	.04618	.02790	.27734	.85578	1.00000

TABLE 4.08: VAULT: ROTATED PC MATRIX

	FACTOR 1	FACTOR 2	FACTOR 3
V4	.94102	.15069	.21674
V3	.90875	.24704	.22959
V10	.83368	.38163	.16802
V1	.58525	.56563	.24749
V5	.22660	.95916	.04505
V6	.26898	.94706	.00577
V12	.21155	-.05907	.94479
V11	.22489	.16986	.92691

TABLE 4.09: FACE: CORRELATION MATRIX

	F1	F2	F3	F4	F8	F9
F1	1.00000					
F2	.51732	1.00000				
F3	.87847	.23278	1.00000			
F4	.71341	.21197	.69328	1.00000		
F8	.95602	.54786	.85124	.74639	1.00000	
F9	.82816	.33786	.73096	.51484	.83087	1.00000
F10	.70358	.16017	.66393	.75600	.74042	.63658
F11	.86623	.26884	.80034	.73749	.89768	.90296
F12	.72807	.08953	.65187	.83120	.74014	.67432
F13	.65226	.08005	.58514	.82818	.68373	.59684
F21	.83361	.38668	.73986	.59906	.82015	.82728
F23	.73578	.38886	.67229	.58670	.77683	.86904

	F10	F11	F12	F13	F21	F23
F10	1.00000					
F11	.86008	1.00000				
F12	.85408	.80980	1.00000			
F13	.85636	.78457	.98244	1.00000		
F21	.71446	.81194	.79227	.74592	1.00000	
F23	.67175	.83558	.66833	.65044	.78182	1.00000

TABLE 4.10: FACE: ROTATED PC MATRIX

	FACTOR 1	FACTOR 2	FACTOR 3
F9	.92752	.26447	.13042
F23	.80875	.34964	.18405
F11	.77642	.56824	.11248
F21	.73950	.47808	.22067
F3	.71714	.44794	.17135
F1	.71134	.47831	.42986
F8	.69371	.51373	.45320
F13	.37496	.89411	-.02384
F4	.27288	.87170	.21407
F12	.45694	.85929	-.01481
F10	.47416	.78302	.04209
F2	.21493	-.01467	.95732

TABLE 4.11: REGIONAL COMBINATION: CORRELATION MATRIX

	B6	B8	B9	V1	V2	F1	F4
B6	1.00000						
B8	.48548	1.00000					
B9	.66626	.48123	1.00000				
V1	.42610	.24419	.63979	1.00000			
V2	.47500	.55069	.69963	.85016	1.00000		
F1	.33678	.48997	.24569	.29772	.21936	1.00000	
F4	.03226	.39253	-.02951	.01366	.07602	.71341	1.00000

TABLE 4.12: REGIONAL COMBINATION: ROTATED PC MATRIX

	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
V1	.95276	.11246	.21745	-.06145
V2	.88207	.02932	.18703	.38633
F4	-.02916	.91092	-.13273	.21930
F1	.14494	.90556	.26369	.07950
B6	.22176	.09917	.91609	.18178
B9	.59405	-.02423	.63193	.25934
B8	.18834	.31606	.28388	.87099

APPENDIX 4B: MATRICES OF CORRELATIONS BETWEEN CHARACTERS AND CANONICAL DISCRIMINANT FUNCTIONS

TABLE 4.13: MANDIBLE:
CORRELATIONS BETWEEN DISCRIMINATING VARIABLES AND CANONICAL DISCRIMINANT FUNCTIONS (VARIABLES ORDERED BY SIZE OF CORRELATION WITHIN FUNCTION)

	FUNC 1	FUNC 2	FUNC 3
M12	0.81197	0.28573	-0.02517
M7	0.29090	0.66541	-0.42573
M9	-0.11931	0.63169	-0.15301
M10	0.33921	0.55389	0.30938
M5	0.35089	0.33299	0.50506
M2	0.05862	0.23741	0.16126
M8	-0.19314	0.36623	0.54067
M11	0.35737	0.36644	0.42356

TABLE 4.14: PALATE:
CORRELATIONS BETWEEN DISCRIMINATING VARIABLES AND CANONICAL DISCRIMINANT FUNCTIONS (VARIABLES ORDERED BY SIZE OF CORRELATION WITHIN FUNCTION)

	FUNC 1	FUNC 2	FUNC 3
P3	0.87917	0.06938	0.32825
P1	0.77320	-0.05947	0.29081
P2	0.05672	0.16226	0.72637
P7	0.23296	0.18368	0.27853
P4	0.27289	0.59442	0.28093
P9	0.40162	-0.26945	0.20262

TABLE 4.15: BASE:
CORRELATIONS BETWEEN DISCRIMINATING VARIABLES AND CANONICAL DISCRIMINANT FUNCTIONS (VARIABLES ORDERED BY SIZE OF CORRELATION WITHIN FUNCTION)

	FUNC 1	FUNC 2	FUNC 3
B3	-0.17219	0.66995	-0.09466
B4	0.24446	0.64797	0.03904
B13	-0.08910	0.51120	-0.45468
B9	0.31417	0.42558	0.02413
B7	0.25724	0.52848	0.61495
B11	-0.31538	0.33189	-0.04788
B6	0.29527	0.37781	0.02235
B10	-0.31904	0.49407	-0.11909
B12	-0.13531	0.48752	-0.11538
B8	0.10634	0.41036	-0.05088
B5	0.34351	0.43792	0.05427

TABLE 4.16: VAULT:
CORRELATIONS BETWEEN DISCRIMINATING VARIABLES AND CANONICAL DISCRIMINANT FUNCTIONS (VARIABLES ORDERED BY SIZE OF CORRELATION WITHIN FUNCTION)

	FUNC 1	FUNC 2	FUNC 3
V10	0.56296	-0.22310	0.00361
V3	0.47932	0.38093	-0.17587
V1	0.53601	-0.31931	-0.73453
V11	0.37755	0.03188	0.36006
V12	0.33886	0.27971	0.30650
V6	0.39304	-0.13695	-0.06022
V5	0.42572	-0.19434	-0.08510
V4	0.46210	0.24225	-0.18735

TABLE 4.17: FACE:
CORRELATIONS BETWEEN DISCRIMINATING VARIABLES AND CANONICAL DISCRIMINANT FUNCTIONS (VARIABLES ORDERED BY SIZE OF CORRELATION WITHIN FUNCTION)

	FUNC 1	FUNC 2	FUNC 3
F13	0.69694	-0.05902	0.07532
F11	0.57921	-0.07928	0.35337
F1	0.40204	0.59669	0.35186
F9	0.40637	-0.01995	0.57345
F21	0.44115	-0.12785	0.52588
F2	0.04391	0.35320	-0.02084
F8	0.41421	0.39454	0.19230
F3	0.31826	0.31062	0.31519
F12	0.54200	-0.10011	0.12881
F23	0.42563	0.14239	0.29066
F4	0.41230	-0.12419	0.15870
F10	0.50001	-0.11801	-0.10271

TABLE 4.18: REGIONAL COMBINATION:
CORRELATIONS BETWEEN DISCRIMINATING VARIABLES AND CANONICAL DISCRIMINANT FUNCTIONS (VARIABLES ORDERED BY SIZE OF CORRELATION WITHIN FUNCTION)

	FUNC 1	FUNC 2	FUNC 3
V1	0.82751	0.05116	-0.04236
V2	0.67679	0.10133	0.33870
F1	0.21406	0.90556	0.23105
B9	0.33607	0.26162	0.62725
F4	-0.15855	0.30931	0.52278
B6	0.24835	0.11520	0.56746
B8	0.11289	0.35193	0.29004

APPENDIX 4C: HOMINOIDS: WITHIN-GROUP CORRELATION MATRICES

TABLE 4.19: HOMO SAPIENS: CORRELATION MATRIX: MANDIBLE

	M1	M2	M3	M4	M5	M6
M1	1.00000					
M2	.54077	1.00000				
M3	.58986	.60411	1.00000			
M4	.65574	.46166	.33961	1.00000		
M5	.45757	.55950	.61064	.42817	1.00000	
M6	.45815	.52897	.46450	.64880	.58426	1.00000
M7	.66113	.28633	.62445	.50861	.50023	.37218
M8	.70741	.45401	.42629	.58944	.32400	.35747
M9	.78476	.56665	.49340	.67395	.35750	.51125
M10	.39061	.58160	.42439	.30412	.84367	.61410
M11	.37273	.65357	.50607	.19749	.76176	.37914
M12	.27384	.23528	.24057	.25003	.43157	.15245

	M7	M8	M9	M10	M11	M12
M7	1.00000					
M8	.40191	1.00000				
M9	.47608	.91058	1.00000			
M10	.23387	.29090	.32179	1.00000		
M11	.31531	.15707	.22041	.86955	1.00000	
M12	.41493	.66506	.58182	.44442	.27446	1.00000

TABLE 4.20: PAN: CORRELATION MATRIX: MANDIBLE

	M1	M2	M3	M4	M5	M6
M1	1.00000					
M2	.34183	1.00000				
M3	.60949	.54027	1.00000			
M4	.43964	.20136	.66175	1.00000		
M5	.45074	.19703	.75033	.44240	1.00000	
M6	.23332	-.10394	.21592	.59322	.17682	1.00000
M7	.12646	.27012	.51060	.42808	.28782	-.00087
M8	.57427	.37795	.40653	.15193	.20624	-.07568
M9	.33310	.70082	.70885	.28364	.39579	-.09366
M10	.28935	.31961	.71732	.68235	.45301	.39995
M11	.11372	.14605	.49190	.55140	.34658	.43045
M12	.44666	.29543	.57761	.20307	.51602	-.06390

	M7	M8	M9	M10	M11	M12
M7	1.00000					
M8	-.01671	1.00000				
M9	.38058	.50658	1.00000			
M10	.53570	.01836	.59665	1.00000		
M11	.28849	-.15714	.32210	.83403	1.00000	
M12	.05300	.28479	.53400	.45906	.40930	1.00000

TABLE 4.21: GORILLA: CORRELATION MATRIX: MANDIBLE

	M1	M2	M3	M4	M5	M6
M1	1.00000					
M2	.61449	1.00000				
M3	.70100	.71852	1.00000			
M4	.72741	.80518	.88189	1.00000		
M5	.67267	.37858	.78821	.62897	1.00000	
M6	.79234	.74133	.76898	.88269	.63478	1.00000
M7	.39796	.26366	.47820	.57303	.53510	.62987
M8	.43730	.48342	.40794	.27821	.17025	.24085
M9	.53537	.49646	.59131	.51342	.40113	.52698
M10	.66729	.56503	.76035	.75591	.79724	.79525
M11	.79745	.72631	.77171	.83861	.62138	.87633
M12	.72248	.67948	.82685	.87548	.64303	.85767

	M7	M8	M9	M10	M11	M12
M7	1.00000					
M8	-.15563	1.00000				
M9	.33344	.44260	1.00000			
M10	.70659	-.02490	.41066	1.00000		
M11	.46437	.31993	.48174	.83660	1.00000	
M12	.66100	.23992	.56853	.78454	.82952	1.00000

TABLE 4.22: PONGO: CORRELATION MATRIX: MANDIBLE

	M1	M2	M3	M4	M5	M6
M1	1.00000					
M2	.78020	1.00000				
M3	.83707	.66408	1.00000			
M4	.77266	.81237	.90139	1.00000		
M5	.64904	.45315	.78200	.64539	1.00000	
M6	.80170	.71169	.76843	.76060	.64938	1.00000
M7	.42618	.50091	.50495	.63727	.23676	.20314
M8	.56469	.55059	.44849	.39135	.30363	.55767
M9	.70779	.68582	.75391	.73690	.48969	.59562
M10	.71600	.61681	.74896	.69527	.79157	.76115
M11	.67973	.70526	.64859	.67285	.67942	.82008
M12	.65410	.59435	.83541	.77212	.60637	.63018

	M7	M8	M9	M10	M11	M12
M7	1.00000					
M8	.06899	1.00000				
M9	.55922	.61109	1.00000			
M10	.35016	.34354	.52443	1.00000		
M11	.18775	.40006	.48136	.84618	1.00000	
M12	.50956	.34083	.76011	.57134	.56324	1.00000

TABLE 4.23: HOMO SAPIENS: CORRELATION MATRIX: PALATE

	P1	P2	P3	P4	P5	P6
P1	1.00000					
P2	.51582	1.00000				
P3	.92640	.68886	1.00000			
P4	.55217	.71103	.64721	1.00000		
P5	.44454	-.15976	.45170	.24798	1.00000	
P6	.78015	.74990	.89786	.93207	.36670	1.00000
P7	.39915	-.28937	.59107	.10245	.28516	.22228
P8	.15273	.23379	.21834	.50423	-.29070	.33252
P9	.70047	.70439	.69640	.75562	.22076	.75136

	P7	P8	P9
P7	1.00000		
P8	.52729	1.00000	
P9	.14940	.36034	1.00000

TABLE 4.24: PAN: CORRELATION MATRIX: PALATE

	P1	P2	P3	P4	P5	P6
P1	1.00000					
P2	.34476	1.00000				
P3	.84319	.66370	1.00000			
P4	.39496	.80422	.61522	1.00000		
P5	.46755	.36461	.41520	.50791	1.00000	
P6	.48906	.86466	.71536	.91539	.51517	1.00000
P7	.36828	.32201	.47952	.33719	.29456	.41257
P8	.50678	.30871	.64531	.29860	.26226	.43357
P9	.58754	.66540	.73928	.54318	.43830	.61927

	P7	P8	P9
P7	1.00000		
P8	.78120	1.00000	
P9	.39856	.51189	1.00000

TABLE 4.25: GORILLA: CORRELATION MATRIX: PALATE

	P1	P2	P3	P4	P5	P6
P1	1.00000					
P2	.79644	1.00000				
P3	.92429	.72054	1.00000			
P4	.78103	.90750	.76919	1.00000		
P5	.87949	.70419	.93617	.77899	1.00000	
P6	.82719	.89243	.77756	.96647	.77961	1.00000
P7	.32577	.39898	.40177	.44693	.53021	.39346
P8	.29633	.47800	.31813	.47019	.36307	.42854
P9	.60169	.81565	.57566	.67283	.69041	.59523

	P7	P8	P9
P7	1.00000		
P8	.66324	1.00000	
P9	.32719	.33158	1.00000

TABLE 4.26: PONGO: CORRELATION MATRIX: PALATE

	P1	P2	P3	P4	P5	P6
P1	1.00000					
P2	.79229	1.00000				
P3	.96912	.71231	1.00000			
P4	.90271	.91587	.84844	1.00000		
P5	.80427	.52500	.86622	.64104	1.00000	
P6	.89180	.96270	.82472	.96087	.68002	1.00000
P7	.47060	.33934	.48123	.34308	.38938	.36170
P8	.75090	.53165	.77302	.63811	.64445	.60318
P9	.79090	.85101	.72630	.84526	.56256	.87955

	P7	P8	P9
P7	1.00000		
P8	.84380	1.00000	
P9	.19852	.40368	1.00000

TABLE 4.27: HOMO SAPIENS: CORRELATION MATRIX: BASE

	B1	B2	B3	B4	B5	B6
B1	1.00000					
B2	.43259	1.00000				
B3	.29454	.50174	1.00000			
B4	.35711	.62872	.89404	1.00000		
B5	.53917	.66307	.83626	.91895	1.00000	
B6	.29266	.53035	.89825	.90478	.86950	1.00000
B7	.14293	.20702	.26943	.40789	.45792	.26608
B8	.41596	.39105	.76064	.78298	.66801	.74985
B9	.01561	.20980	.31824	.33583	.23688	.38275
B10	.18920	.27932	.60117	.39591	.31135	.35308
B11	.28102	-.03773	.22979	.17781	.17203	.28923
B12	.66428	-.03214	.44586	.33631	.46302	.29107
B13	.33251	-.01998	.05473	.00283	.14321	.00301
B14	.29193	.19587	.36701	.46300	.48073	.25975
B15	.00628	-.03783	.25262	.32837	.15239	.29740
B16	.07315	.62059	.64059	.71336	.70302	.72888
B17	.12429	.36635	.76166	.77794	.71289	.69203
B18	.04641	.37511	.72069	.58176	.49018	.55457
B19	.30109	.27203	.71342	.72007	.60500	.62691
B20	-.17858	.00901	.27177	.18690	-.00252	.12787
B21	.30494	.57243	.50457	.60602	.55683	.52139
B22	.38551	.23259	.58804	.65744	.62520	.59524
B23	-.16105	-.10036	.39848	.31048	.24974	.34263
B24	.51697	.39195	.21286	.29890	.42495	.15479

	B7	B8	B9	B10	B11	B12
B7	1.00000					
B8	.32247	1.00000				
B9	.28008	.33906	1.00000			
B10	-.04604	.35822	.24128	1.00000		
B11	-.33863	.22057	.51701	.09734	1.00000	
B12	.31696	.35096	-.01857	.48655	.19906	1.00000
B13	.16814	-.08553	-.02014	.23193	.29248	.61178
B14	.43989	.37010	.08786	.25565	-.16457	.41887
B15	.34099	.56857	.34084	.18429	.26033	.22781
B16	.20079	.40840	.30248	.24091	-.01672	.07784
B17	.19552	.57556	.45040	.38301	.15735	.23766
B18	.11947	.42827	.41530	.70558	.21561	.37742
B19	-.07905	.56671	.28739	.52418	.21317	.40855
B20	-.53240	.13928	.47138	.47635	.25027	.01401
B21	.04300	.27977	-.01259	.36815	.19264	.10968
B22	.09395	.50310	.38626	.46286	.27564	.53338
B23	.22022	.27237	.04452	.23543	.12486	.06418
B24	.11849	.08277	.21868	.31575	.28475	.36447

TABLE 4.27: HOMO SAPIENS: CORRELATION MATRIX: BASE CONTINUED

	B13	B14	B15	B16	B17	B18
B13	1.00000					
B14	-.13146	1.00000				
B15	.19869	.30205	1.00000			
B16	.01618	.21965	.05673	1.00000		
B17	-.20628	.50237	.18784	.65411	1.00000	
B18	.31723	.23219	.32557	.42915	.38194	1.00000
B19	-.02136	.28398	.12620	.43270	.68257	.50796
B20	-.05885	-.13034	-.00328	.28778	.45659	.31647
B21	-.15023	.37560	-.12084	.38460	.30704	.32216
B22	.01325	.63282	.33107	.53726	.72854	.28381
B23	-.38877	.50927	.27290	.04750	.41671	.29890
B24	.40693	.13043	-.08523	.26364	.28804	.25551

	B19	B20	B21	B22	B23	B24
B19	1.00000					
B20	.55657	1.00000				
B21	.47825	.01096	1.00000			
B22	.66896	.38054	.45147	1.00000		
B23	.26041	-.12155	.40335	.34551	1.00000	
B24	.33298	.09261	.23681	.21036	.02770	1.00000

TABLE 4.28: PAN: CORRELATION MATRIX: BASE

	B1	B2	B3	B4	B5	B6
B1	1.00000					
B2	.35780	1.00000				
B3	.29620	.31872	1.00000			
B4	.24002	.35695	.81383	1.00000		
B5	.34495	.50302	.76183	.89948	1.00000	
B6	.28730	.22015	.55631	.61599	.53778	1.00000
B7	.07219	.29707	.37543	.49616	.55414	.36754
B8	.03815	.26038	.52656	.50394	.60870	.21370
B9	.01658	.38589	.47798	.40594	.50376	.21247
B10	.15004	.12747	.88945	.71238	.55298	.30205
B11	.33749	.01471	.39140	.38455	.25243	.52507
B12	-.05656	-.09388	.40925	.20152	.22657	.02530
B13	.03797	-.42414	.23754	.04377	-.02700	-.04795
B14	.10609	.16416	.44021	.38999	.50430	.18863
B15	-.00039	-.21762	.19754	.20662	.19961	.13875
B16	-.17514	.16743	.32388	.31001	.35855	-.05885
B17	.25885	.33321	.80055	.67668	.69893	.37523
B18	.50860	.26375	.59246	.45595	.50428	.35059
B19	.22060	.11682	.60691	.31287	.36922	.21475
B20	-.19988	-.42537	-.06699	-.17710	-.34982	-.09732
B21	.30415	.74340	.44331	.41767	.60382	.30393
B22	.33021	.56523	.57148	.59680	.73175	.39020
B23	.09278	-.25337	.32930	.12718	.18542	-.07372
B24	-.31542	.00601	.00397	-.16333	-.10421	.07246

	B7	B8	B9	B10	B11	B12
B7	1.00000					
B8	.39920	1.00000				
B9	.63702	.72632	1.00000			
B10	.27827	.40909	.39124	1.00000		
B11	.11899	.20175	.16992	.31405	1.00000	
B12	.25702	.53287	.52015	.45508	.20637	1.00000
B13	-.03686	.14247	-.05515	.36144	.39522	.63826
B14	.42604	.72137	.59179	.33922	.18046	.74077
B15	.14705	.27735	-.09094	.19880	.14616	.39385
B16	.01989	.19643	.21763	.32610	-.21093	-.00002
B17	.39401	.54645	.50741	.71929	.20531	.41353
B18	.35548	.49676	.40302	.51481	.25912	.30484
B19	.21703	.35128	.29123	.51921	.08889	.26654
B20	-.10470	-.03327	-.05740	.15690	-.28329	.30104
B21	.38167	.38133	.56811	.24361	.20724	.01246
B22	.52212	.55157	.61163	.37623	.48690	.30467
B23	-.19070	-.03737	-.21270	.35046	.15199	.36319
B24	.18153	.21552	.25396	.00218	-.25208	.06849

TABLE 4.28: PAN: CORRELATION MATRIX: BASE CONTINUED

	B13	B14	B15	B16	B17	B18
B13	1.00000					
B14	.24328	1.00000				
B15	.51198	.45001	1.00000			
B16	-.13473	.23135	.16791	1.00000		
B17	.04849	.68813	.36424	.52397	1.00000	
B18	.36419	.36092	.22081	.19749	.40945	1.00000
B19	.35048	.27289	.18904	.26523	.50656	.72779
B20	.13612	.12131	.26150	.07883	.07065	-.04092
B21	-.30569	.25169	-.41612	.24462	.33192	.42184
B22	-.01537	.62782	.13060	.30037	.59579	.45234
B23	.73172	.10185	.41003	.25616	.13722	.32360
B24	-.05445	.14500	-.02867	.00343	.06869	-.00669

	B19	B20	B21	B22	B23	B24
B19	1.00000					
B20	-.14396	1.00000				
B21	.23485	-.54766	1.00000			
B22	.22263	-.46094	.77023	1.00000		
B23	.41281	-.15117	-.05850	.12431	1.00000	
B24	.07564	.11670	.04273	-.05906	-.18438	1.00000

TABLE 4.29: GORILLA: CORRELATION MATRIX: BASE

	B1	B2	B3	B4	B5	B6
B1	1.00000					
B2	.67290	1.00000				
B3	.53781	.73091	1.00000			
B4	.23260	.68924	.86154	1.00000		
B5	.47775	.82216	.73883	.80056	1.00000	
B6	.48672	.70485	.75790	.72065	.78787	1.00000
B7	.49724	.85592	.77149	.81962	.83394	.66330
B8	.13969	.61331	.55502	.74694	.63345	.44401
B9	.34662	.57119	.57665	.60028	.51161	.54022
B10	.46973	.52121	.87243	.68453	.46999	.39911
B11	.49060	.56449	.58838	.50372	.58956	.81086
B12	.41154	.56027	.75275	.53928	.54763	.62470
B13	.48224	.51673	.81381	.57696	.52552	.58398
B14	.42947	.59196	.66548	.55396	.55445	.59277
B15	.55704	.76653	.68596	.57112	.60129	.57944
B16	.61060	.66612	.76224	.53139	.66356	.56451
B17	.68509	.81417	.91570	.75088	.74851	.73583
B18	.55274	.76270	.93184	.81294	.77704	.74901
B19	.59685	.77953	.81686	.66208	.67191	.68509
B20	.69253	.78708	.84530	.60022	.70344	.77469
B21	.44251	.55834	.73407	.58578	.64463	.77726
B22	.46142	.67526	.79854	.65078	.67903	.76548
B23	.34134	.22468	.32394	.15525	.08394	.23913
B24	.28418	.33875	.31448	.26773	.16928	.36403

	B7	B8	B9	B10	B11	B12
B7	1.00000					
B8	.73009	1.00000				
B9	.56967	.75801	1.00000			
B10	.62357	.49034	.42720	1.00000		
B11	.50453	.40425	.61936	.26774	1.00000	
B12	.56888	.26746	.38577	.63073	.56614	1.00000
B13	.65443	.31423	.42021	.78374	.51402	.82553
B14	.44673	.31364	.46722	.45576	.58564	.82058
B15	.60122	.36710	.37100	.48967	.49944	.61829
B16	.54752	.22217	.32599	.57952	.52901	.69081
B17	.73341	.47510	.52561	.74189	.67765	.75191
B18	.75740	.52736	.45342	.80345	.53878	.74883
B19	.57455	.33639	.34329	.60978	.60190	.64526
B20	.65066	.29201	.39907	.63285	.65687	.81682
B21	.54426	.35396	.56851	.47489	.80233	.77332
B22	.60891	.41104	.56191	.55442	.75008	.88447
B23	.21397	-.30564	-.02128	.22363	.20008	.45786
B24	.28946	.32874	.23369	.21869	.43092	-.11128

TABLE 4.29: GORILLA: CORRELATION MATRIX: BASE CONTINUED

	B13	B14	B15	B16	B17	B18
B13	1.00000					
B14	.50827	1.00000				
B15	.46069	.79370	1.00000			
B16	.65991	.71834	.67065	1.00000		
B17	.73283	.76453	.78783	.87936	1.00000	
B18	.74767	.68400	.66578	.77076	.91229	1.00000
B19	.55296	.73542	.78982	.87176	.93692	.84277
B20	.75330	.75264	.74899	.88564	.91647	.83065
B21	.71663	.69831	.43378	.74290	.74544	.72585
B22	.71326	.88971	.72296	.76598	.81198	.78107
B23	.32297	.42768	.39613	.40025	.42872	.33664
B24	.05568	-.09976	.23572	.07639	.28950	.23179

	B19	B20	B21	B22	B23	B24
B19	1.00000					
B20	.87679	1.00000				
B21	.66663	.78065	1.00000			
B22	.75757	.83059	.90001	1.00000		
B23	.44643	.44422	.32180	.37212	1.00000	
B24	.32058	.20581	.16277	.10850	-.01030	1.00000

TABLE 4.30: PONGO: CORRELATION MATRIX: BASE

	B1	B2	B3	B4	B5	B6
B1	1.00000					
B2	.38182	1.00000				
B3	.05309	-.06616	1.00000			
B4	.09382	.15909	.74391	1.00000		
B5	-.18659	.06415	.60237	.82701	1.00000	
B6	-.05258	-.08273	.78214	.85854	.80486	1.00000
B7	.33933	.03055	.60047	.63792	.37913	.62252
B8	.15202	-.01471	.79706	.76246	.65073	.81964
B9	.51685	-.05599	.55030	.20393	-.00358	.25535
B10	.21722	-.02221	.83759	.43508	.23545	.41431
B11	-.22168	-.02106	.76361	.73275	.68682	.75717
B12	.18469	.00460	.73805	.63276	.47000	.65468
B13	.25277	-.17692	.59236	.42020	.20387	.45894
B14	-.07666	-.04193	.78928	.69102	.60828	.73266
B15	-.14355	-.36085	.72481	.55351	.48407	.69551
B16	.07396	-.21892	.88679	.57443	.50946	.63823
B17	.01493	-.09353	.93588	.67345	.61806	.73208
B18	.10735	.04649	.90427	.57572	.43158	.57608
B19	-.07717	.06469	.85126	.63772	.57520	.68303
B20	.20249	-.14315	.76426	.50488	.49194	.67240
B21	-.04349	-.07195	.85048	.64568	.57578	.74677
B22	-.10916	-.20628	.85045	.64731	.59187	.78513
B23	.15273	.12124	.52550	.10748	.06572	.23439
B24	-.32636	.04538	.19276	.24663	.37139	.12194

	B7	B8	B9	B10	B11	B12
B7	1.00000					
B8	.80992	1.00000				
B9	.62527	.53454	1.00000			
B10	.42751	.56613	.55390	1.00000		
B11	.35894	.58821	.03811	.63394	1.00000	
B12	.54078	.75933	.38394	.69846	.77615	1.00000
B13	.42302	.55392	.35370	.71080	.66587	.86765
B14	.50752	.79341	.29684	.68094	.82904	.86415
B15	.43586	.65846	.37170	.54948	.59691	.55061
B16	.59747	.72980	.54133	.80321	.63122	.60693
B17	.63352	.82744	.56807	.74670	.66549	.72464
B18	.50546	.62845	.57043	.82487	.59044	.58465
B19	.64724	.72121	.47318	.68835	.67866	.54975
B20	.61384	.68042	.69756	.55368	.40747	.46258
B21	.58101	.83086	.35516	.76474	.81902	.83621
B22	.57815	.81729	.38022	.70242	.79657	.78928
B23	.33136	.51177	.47069	.69444	.40277	.61998
B24	-.03887	.08795	-.33926	.19991	.28703	-.03939

TABLE 4.30: PONGO: CORRELATION MATRIX: BASE CONTINUED

	B13	B14	B15	B16	B17	B18
B13	1.00000					
B14	.75985	1.00000				
B15	.56383	.81907	1.00000			
B16	.53796	.72137	.73138	1.00000		
B17	.52060	.77263	.66630	.88138	1.00000	
B18	.48975	.64447	.57945	.82284	.89088	1.00000
B19	.43812	.70797	.61722	.81763	.87837	.85788
B20	.36865	.53586	.64852	.77620	.81964	.71624
B21	.75141	.93497	.76485	.82671	.84846	.74959
B22	.71372	.94798	.88505	.84007	.83775	.71785
B23	.59230	.64159	.40806	.59351	.57762	.51362
B24	-.12791	.15839	.03065	.28496	.20360	.29151

	B19	B20	B21	B22	B23	B24
B19	1.00000					
B20	.77707	1.00000				
B21	.81999	.63848	1.00000			
B22	.78522	.67616	.96502	1.00000		
B23	.56238	.45302	.67821	.61113	1.00000	
B24	.24700	-.12156	.22938	.18335	-.04386	1.00000

TABLE 4.31: HOMO SAPIENS: CORRELATION MATRIX: VAULT

	V1	V2	V3	V4	V5	V6
V1	1.00000					
V2	.74703	1.00000				
V3	.58601	.48431	1.00000			
V4	.65611	.50202	.93489	1.00000		
V5	.49871	.35745	.20119	.37579	1.00000	
V6	.36817	.20875	.15841	.36927	.91451	1.00000
V7	.46122	.16408	.03174	.11897	.09225	.08675
V8	.56203	.27681	.22103	.29384	.17434	.08738
V9	.58173	.54053	.61236	.69986	.50963	.35898
V10	.60873	.48705	.89581	.90441	.17353	.20373
V11	.25855	.21880	-.05963	.06816	.02451	-.00460
V12	.17797	.14082	-.18961	-.06173	-.06845	-.12757
V13	.36847	.16820	.22690	.20912	.22318	.23328
V14	.21619	-.02716	.23982	.20012	.24703	.29927
V15	.29383	.19285	.45788	.50801	-.04597	.05259
V16	.35095	.17621	.35272	.41126	.02792	.17518
V17	.71286	.68006	.20703	.31192	.34773	.27395
V18	.56423	.47459	.41106	.47181	.41840	.46486
V19	.40025	.20744	.49961	.52409	.41404	.43206
V20	.26052	.16545	.23457	.23501	.22228	.19149
V21	.60461	.50708	.33684	.49019	.56118	.60554
V22	.49992	.71154	.07372	.18698	.19191	.12880
V23	.32553	.33254	.49861	.45250	.32290	.26949
V24	.16869	.25432	-.04695	.10849	.31136	.30654

	V7	V8	V9	V10	V11	V12
V7	1.00000					
V8	.81013	1.00000				
V9	.08007	.37013	1.00000			
V10	.04231	.17105	.50920	1.00000		
V11	.64213	.54129	.25880	.03351	1.00000	
V12	.62658	.50385	.18663	-.13542	.95285	1.00000
V13	.30453	.32913	-.07423	.17723	-.45944	-.48788
V14	.15525	.15467	-.11247	.18525	-.59630	-.66046
V15	.05994	.02254	.32757	.40676	.03166	.05352
V16	.17672	.18764	.28071	.28457	.11017	.11699
V17	.46676	.56222	.44575	.22865	.34221	.28776
V18	.27039	.29779	.43879	.36189	.22118	.11937
V19	.01182	.28214	.44143	.37527	-.11988	-.16819
V20	-.07740	.20128	.52499	.11054	-.02781	-.06746
V21	.48593	.58157	.43924	.32779	.30114	.19987
V22	.25362	.30122	.48164	.12203	.49199	.49911
V23	.34688	.20387	.33527	.32868	.23033	.15062
V24	.25596	.43774	.42810	-.04937	.46565	.41272

TABLE 4.31: HOMO SAPIENS: CORRELATION MATRIX: VAULT CONTINUED

	V13	V14	V15	V16	V17	V18
V13	1.00000					
V14	.93384	1.00000				
V15	-.05631	-.04696	1.00000			
V16	-.02152	-.04733	.81456	1.00000		
V17	.27723	.09081	.36253	.38960	1.00000	
V18	.16889	.07604	.61059	.70008	.66162	1.00000
V19	.25671	.20521	.39855	.58737	.34046	.73700
V20	.08186	.01111	.13647	.39110	.29996	.55221
V21	.36111	.23192	.31997	.46381	.72497	.79072
V22	-.15377	-.38646	.31164	.37267	.78444	.54732
V23	.14212	.12693	-.04655	.01671	.10109	.25454
V24	-.19291	-.23787	.16407	.29435	.48350	.37375

	V19	V20	V21	V22	V23	V24
V19	1.00000					
V20	.68057	1.00000				
V21	.60075	.34065	1.00000			
V22	.22230	.30172	.50985	1.00000		
V23	.15130	.01289	.36150	.12395	1.00000	
V24	.21846	.25895	.55058	.44401	.00118	1.00000

TABLE 4.32: PAN: CORRELATION MATRIX: VAULT

	V1	V2	V3	V4	V5	V6
V1	1.00000					
V2	.10473	1.00000				
V3	.32386	.31493	1.00000			
V4	.38841	.48003	.91502	1.00000		
V5	-.10771	.13701	-.14929	-.21393	1.00000	
V6	-.17832	.21315	-.11603	-.16760	.98056	1.00000
V7	.16782	.48987	.38583	.38653	-.23953	-.20121
V8	.10520	.41438	.26644	.28830	-.16571	-.14038
V9	.52977	.60663	.29726	.44473	.23118	.27044
V10	.35721	.21508	.70763	.78366	-.21612	-.16078
V11	.25571	.02321	-.24918	-.32995	-.27273	-.29977
V12	.07445	.20287	-.26270	-.29113	-.14999	-.15655
V13	-.10038	.38936	.50783	.58087	.02318	.09178
V14	-.17809	.31581	.53315	.53770	.01184	.09023
V15	.16602	.40381	.65664	.63103	.11170	.18455
V16	.07862	.46070	.51557	.48432	.11560	.19987
V17	.14524	.70592	.50878	.67103	-.03554	.02295
V18	.19721	.56609	.62312	.67384	.14133	.22014
V19	.07955	.56790	.54423	.57312	.18523	.27109
V20	.20951	.55284	.60251	.66906	-.03311	.03195
V21	.21865	.77668	.68265	.73335	.14865	.23766
V22	.50098	.62194	.62629	.73703	-.09524	-.07129
V23	.07009	.11094	-.24907	-.13657	.13331	.12269
V24	.09718	.26188	-.15264	-.08201	.12481	.15154

	V7	V8	V9	V10	V11	V12
V7	1.00000					
V8	.93911	1.00000				
V9	.41288	.34911	1.00000			
V10	.04702	-.00930	.26206	1.00000		
V11	.41108	.25153	.09519	-.43855	1.00000	
V12	.35637	.15142	.18835	-.44288	.90837	1.00000
V13	.59101	.67066	.28218	.30050	-.50684	-.53012
V14	.62891	.68854	.22577	.31409	-.46802	-.47807
V15	.33583	.24181	.43997	.53829	-.37532	-.31230
V16	.45249	.40502	.52461	.31704	-.26642	-.20292
V17	.44424	.45802	.54711	.33369	-.24306	-.11085
V18	.19154	.15427	.59708	.56295	-.37262	-.26543
V19	.19373	.13332	.54279	.40853	-.35945	-.22266
V20	.33245	.24308	.60226	.45093	-.17889	-.03701
V21	.56016	.45172	.64268	.55538	-.16863	-.04567
V22	.42194	.34559	.64827	.55822	.00900	.08606
V23	.35276	.47565	.48749	-.29322	.16774	.19882
V24	.44142	.52772	.55650	-.32315	.29977	.28391

TABLE 4.32: PAN: CORRELATION MATRIX: VAULT CONTINUED

	V13	V14	V15	V16	V17	V18
V13	1.00000					
V14	.95848	1.00000				
V15	.53119	.60535	1.00000			
V16	.56044	.65686	.89428	1.00000		
V17	.56418	.49335	.40701	.52970	1.00000	
V18	.41934	.39831	.66593	.64227	.73705	1.00000
V19	.43145	.42502	.67160	.71006	.71028	.94868
V20	.38808	.39776	.63071	.67051	.76835	.90527
V21	.56039	.59745	.80637	.78432	.68264	.75694
V22	.26203	.22593	.49926	.46640	.76592	.76101
V23	.20565	.21743	-.08150	.22888	.21342	-.09334
V24	.26391	.26805	.05770	.40267	.34772	.14313

	V19	V20	V21	V22	V23	V24
V19	1.00000					
V20	.91755	1.00000				
V21	.72777	.73652	1.00000			
V22	.65926	.81551	.72496	1.00000		
V23	-.06279	.07267	.04235	.10964	1.00000	
V24	.22023	.32274	.19947	.23629	.86728	1.00000

TABLE 4.33: GORILLA: CORRELATION MATRIX: VAULT

	V1	V2	V3	V4	V5	V6
V1	1.00000					
V2	.47255	1.00000				
V3	.25998	-.02847	1.00000			
V4	.24106	-.07823	.93139	1.00000		
V5	-.09274	.18666	-.06967	-.28767	1.00000	
V6	-.09698	.12164	.00514	-.21375	.97493	1.00000
V7	-.04957	-.11257	.40283	.27803	-.17679	-.06923
V8	.25027	.31858	.49207	.38670	.05896	.00398
V9	.16603	.15023	.60096	.43079	.37863	.34317
V10	.23884	-.06896	.56041	.65039	-.39607	-.39353
V11	.35918	.15469	.57360	.57904	-.09995	-.08860
V12	.24031	.04547	.56234	.54695	-.21694	-.19220
V13	.19907	.22030	.68828	.58886	.22691	.21580
V14	.21295	.22841	.68502	.59435	.22634	.21715
V15	.34633	.05087	.78932	.68260	.08803	.12187
V16	.27184	.10489	.79270	.63281	.28292	.30988
V17	.27728	.30508	.75406	.60351	.19810	.21588
V18	.23730	-.00619	.82905	.69291	.16333	.21425
V19	.27989	.16694	.79265	.59461	.19308	.21764
V20	.31194	.12584	.83488	.66140	.20467	.22058
V21	.22875	.20516	.81747	.67456	.31069	.34655
V22	.25010	.22504	.81026	.68999	.16346	.19440
V23	.19474	.06201	.63058	.57142	.15465	.12754
V24	.01845	.15954	.73885	.64722	.18643	.26554

	V7	V8	V9	V10	V11	V12
V7	1.00000					
V8	.03703	1.00000				
V9	.08081	.61099	1.00000			
V10	.12674	.23562	.26467	1.00000		
V11	.16546	.39851	.62197	.31791	1.00000	
V12	.27629	.36257	.57204	.18164	.86719	1.00000
V13	-.02140	.71189	.78205	.10496	.73873	.71973
V14	-.04383	.69069	.78855	.13971	.74937	.71417
V15	.21579	.58046	.79460	.25367	.78120	.85626
V16	.31274	.62127	.83474	.23574	.68881	.72773
V17	.27621	.71581	.83639	.37010	.69084	.68499
V18	.19470	.49052	.72118	.38340	.73543	.68575
V19	.26667	.64155	.76317	.40807	.64501	.60336
V20	.31147	.68184	.80336	.35463	.69904	.66661
V21	.27641	.64577	.79991	.31921	.70227	.63132
V22	.28173	.65408	.84029	.39166	.71557	.73754
V23	.09343	.42561	.74008	.56061	.32681	.33177
V24	.31534	.44632	.67890	.37168	.42219	.41846

TABLE 4.33: GORILLA: CORRELATION MATRIX: VAULT CONTINUED

	V13	V14	V15	V16	V17	V18
V13	1.00000					
V14	.99611	1.00000				
V15	.90427	.90251	1.00000			
V16	.87060	.86763	.94037	1.00000		
V17	.79336	.79225	.86170	.89209	1.00000	
V18	.84720	.84491	.86384	.83876	.81669	1.00000
V19	.76844	.75910	.81044	.82903	.89953	.93571
V20	.84591	.83435	.89746	.91375	.90939	.91066
V21	.85067	.85332	.85934	.94677	.92469	.86670
V22	.83553	.83638	.91086	.91775	.97712	.84918
V23	.49253	.51104	.59471	.62629	.62834	.50361
V24	.55783	.56857	.64657	.68904	.81438	.67575

	V19	V20	V21	V22	V23	V24
V19	1.00000					
V20	.94470	1.00000				
V21	.86696	.90783	1.00000			
V22	.87486	.91367	.92904	1.00000		
V23	.51873	.57941	.59300	.68631	1.00000	
V24	.70762	.68811	.77775	.82412	.65140	1.00000

TABLE 4.34: PONGO: CORRELATION MATRIX: VAULT

	V1	V2	V3	V4	V5	V6
V1	1.00000					
V2	.35030	1.00000				
V3	.24331	-.14229	1.00000			
V4	.34709	-.10341	.97280	1.00000		
V5	.08066	.40680	-.03581	.04902	1.00000	
V6	.13273	.42101	-.00164	.08315	.97815	1.00000
V7	.30638	.43332	.32437	.38515	.08384	.13078
V8	.23097	.56799	.19672	.27338	.17437	.19397
V9	.58308	.51555	.31525	.39310	.19569	.25629
V10	.46021	.00199	.82878	.86834	-.13542	-.11148
V11	-.15664	.48658	-.32951	-.33847	-.02167	-.04970
V12	-.08963	.30540	-.03966	-.05402	-.09314	-.06603
V13	.36278	.18610	.40827	.50284	.07311	.11836
V14	.53467	.21674	.38915	.49982	.20832	.27200
V15	.54218	.34012	.55793	.64436	.33350	.43970
V16	.49046	.28519	.54341	.63486	.29312	.40569
V17	.50433	.32489	.56149	.66785	.45119	.52710
V18	.49445	.56134	.53686	.63300	.53712	.57364
V19	.46137	.47751	.49852	.61719	.55915	.61807
V20	.44986	.46852	.44897	.57847	.62885	.68628
V21	.41200	.41613	.60640	.67931	.53046	.57438
V22	.58718	.44781	.48358	.60045	.55021	.61543
V23	.04099	-.14286	.41923	.42912	.22959	.26562
V24	.23957	.03799	.14898	.22043	.40493	.49758

	V7	V8	V9	V10	V11	V12
V7	1.00000					
V8	.86618	1.00000				
V9	.66094	.59479	1.00000			
V10	.40265	.27407	.33422	1.00000		
V11	.46861	.34801	.15285	-.19807	1.00000	
V12	.63451	.37587	.30018	.00594	.88961	1.00000
V13	.65121	.73420	.64130	.43507	-.20873	-.07832
V14	.49283	.58089	.50484	.48103	-.41188	-.29155
V15	.73239	.58550	.73955	.55113	-.02754	.24320
V16	.73860	.53527	.69388	.57473	.01326	.30972
V17	.66260	.51388	.63671	.59530	-.08298	.14733
V18	.63950	.62130	.73300	.49479	.03272	.14517
V19	.62183	.62487	.63490	.46879	-.03904	.07901
V20	.65945	.63481	.61069	.42868	.03185	.16018
V21	.65985	.55978	.60960	.51308	.06652	.23286
V22	.65651	.60240	.70094	.51203	-.06478	.07645
V23	.24109	-.06759	.18022	.39926	-.17716	.08140
V24	-.02044	-.08489	.32239	.02276	-.38502	-.25713

TABLE 4.34: PONGO: CORRELATION MATRIX: VAULT CONTINUED

	V13	V14	V15	V16	V17	V18
V13	1.00000					
V14	.86864	1.00000				
V15	.63564	.63352	1.00000			
V16	.60052	.62138	.96925	1.00000		
V17	.58002	.63903	.93885	.93256	1.00000	
V18	.60697	.60299	.83516	.77783	.86567	1.00000
V19	.66795	.70199	.84144	.80938	.85637	.94494
V20	.60614	.64895	.85436	.82705	.89045	.92488
V21	.51474	.55803	.84346	.82076	.83742	.90970
V22	.64111	.69103	.90665	.85938	.93748	.89155
V23	.16092	.24842	.42346	.52048	.60267	.32947
V24	.17692	.32706	.46980	.42497	.50937	.41996

	V19	V20	V21	V22	V23	V24
V19	1.00000					
V20	.97203	1.00000				
V21	.92423	.91370	1.00000			
V22	.89816	.93229	.86068	1.00000		
V23	.29301	.33246	.33886	.37997	1.00000	
V24	.46878	.44991	.41286	.50586	.37725	1.00000

TABLE 4.35: HOMO SAPIENS: CORRELATION MATRIX: FACE

	F1	F2	F3	F4	F5	F6
F1	1.00000					
F2	.35694	1.00000				
F3	.67678	-.24182	1.00000			
F4	.12225	.18310	-.06364	1.00000		
F5	.14788	-.13541	.11022	-.16366	1.00000	
F6	.85006	.36262	.49850	.07137	.33527	1.00000
F7	.72756	.10029	.63477	.10030	.34710	.85690
F8	.98484	.39254	.64814	.11749	.15343	.86113
F9	.53076	.30359	.24366	.23243	.21556	.60614
F10	-.08511	-.22184	-.15230	-.41821	.37873	.10418
F11	.45395	.24574	.07918	.11715	.30620	.57258
F12	.53556	.04242	.30270	.07581	.44693	.59646
F13	.65171	.23265	.22501	.10208	.35539	.68011
F14	.30934	.33977	-.04626	.12924	.11753	.45071
F15	-.00443	.31409	-.36813	-.29606	.00107	.12040
F16	.16943	-.23662	.39769	-.22638	.19706	.38630
F17	.66776	.10312	.61071	.03756	.33651	.75195
F18	.47797	.11948	.26207	.26931	.46354	.47054
F19	.34685	-.07588	.34713	-.46275	.29118	.49293
F20	.28886	.06651	.27030	-.49724	.23732	.52034
F21	.33009	.24610	-.02982	.07315	.03799	.45867
F22	.28379	.01014	.21332	-.34709	.43455	.51231
F23	.43068	.21335	.12119	-.01890	.43706	.49472
F24	.61646	.11310	.40466	-.14972	.50282	.77089
F25	.28180	.03257	.28751	-.39610	.25507	.48652
F26	-.03647	-.32287	.11329	.12752	.31118	.11975
F27	.42165	.42622	.27672	.27671	.18701	.61466

	F7	F8	F9	F10	F11	F12
F7	1.00000					
F8	.71901	1.00000				
F9	.68297	.51739	1.00000			
F10	.04930	-.10465	.21428	1.00000		
F11	.56875	.41837	.86672	.58994	1.00000	
F12	.56079	.50000	.59254	.25514	.57577	1.00000
F13	.52014	.63099	.70116	.24403	.68297	.87215
F14	.20431	.36596	.25658	.12515	.28347	.43486
F15	-.15511	.04786	-.32157	.21717	-.10655	.01791
F16	.58248	.17778	.20334	.12049	.14925	.34288
F17	.91720	.64750	.64229	.09410	.56603	.38847
F18	.43166	.47699	.21988	-.42348	.05938	.44470
F19	.31355	.38006	-.12626	.04397	-.09543	.34827
F20	.41287	.29334	-.12408	.04058	-.05487	.27906
F21	.48458	.35112	.62138	.05098	.49823	.65684
F22	.54837	.30701	.51314	.50089	.57604	.51880
F23	.38524	.47316	.23681	-.11980	.14985	.63926
F24	.74606	.64425	.57781	.22331	.55263	.60552
F25	.57335	.32321	.46610	.34766	.44487	.36590
F26	.20296	-.00833	.03444	.00907	-.05920	-.13262
F27	.51339	.43469	.21362	-.25094	.09794	.11170

TABLE 4.35: HOMO SAPIENS: CORRELATION MATRIX: FACE CONTINUED

	F13	F14	F15	F16	F17	F18
F13	1.00000					
F14	.47427	1.00000				
F15	.02049	.44436	1.00000			
F16	.15831	.30321	.11822	1.00000		
F17	.37483	.15017	-.20975	.54347	1.00000	
F18	.45308	.11140	.05876	.19821	.34499	1.00000
F19	.33492	.19198	.45579	.47108	.19557	.60870
F20	.17961	.15909	.54793	.57043	.30281	.48106
F21	.69959	.32823	.13585	.20972	.22359	.43118
F22	.45651	.44076	.13867	.55887	.44937	.07617
F23	.55927	.43363	.31737	.25997	.26666	.82015
F24	.64792	.42620	.10308	.53305	.63983	.51283
F25	.31159	.43958	.13329	.62117	.49373	.03395
F26	-.12495	-.03574	-.26551	.03663	.07847	-.02885
F27	.09758	.11058	.11506	.14618	.46551	.33526

	F19	F20	F21	F22	F23	F24
F19	1.00000					
F20	.83895	1.00000				
F21	.28863	.28531	1.00000			
F22	.28572	.37409	.46734	1.00000		
F23	.57995	.48563	.54803	.45459	1.00000	
F24	.50499	.48379	.53145	.84806	.68837	1.00000
F25	.30980	.40671	.43823	.94876	.39645	.79653
F26	-.10615	-.16548	-.15781	.05090	-.27486	.05359
F27	.24770	.30485	.06096	.04622	.22089	.26411

	F25	F26	F27
F25	1.00000		
F26	.06452	1.00000	
F27	.09997	.24210	1.00000

TABLE 4.36: PAN: CORRELATION MATRIX: FACE

	F1	F2	F3	F4	F5	F6
F1	1.00000					
F2	.67517	1.00000				
F3	.74468	.20392	1.00000			
F4	.44716	.02950	.51586	1.00000		
F5	.12372	.01656	.16617	-.06755	1.00000	
F6	.83454	.69466	.45067	.24689	.09061	1.00000
F7	.52710	.45987	.44316	.26286	.16609	.58154
F8	.91476	.64603	.78788	.35172	.24464	.78888
F9	.62641	.41566	.57174	.05366	.21380	.64276
F10	.63150	.20513	.56872	.29664	.07892	.49762
F11	.71334	.47815	.58766	.14747	.11507	.66073
F12	.54398	.29770	.50501	.52565	-.06995	.45548
F13	.55045	.20315	.56172	.64052	-.04767	.44520
F14	.65735	.56067	.43142	.30487	-.04938	.63006
F15	.03183	-.01460	.19401	.40669	-.24745	-.08608
F16	.34263	-.23512	.58188	.41267	-.14640	.24560
F17	.63301	.46648	.52048	.11879	.23614	.66972
F18	.29995	.37121	.15887	.30474	-.01269	.37730
F19	.31068	.26428	.26195	.28169	.18298	.34794
F20	-.15289	-.14417	-.06466	.31307	-.07686	.04657
F21	.03400	.15037	.05730	-.18164	-.03941	.17848
F22	.46925	.36875	.31621	.21816	.10045	.55589
F23	.41752	.28547	.26289	.36718	.24972	.49948
F24	.55016	.44468	.35794	.36087	.07911	.58161
F25	.48884	.36319	.35448	.24023	.14182	.58086
F26	-.20124	-.08951	-.31052	-.25822	.01755	-.09330
F27	.10103	.19727	.13149	.24146	.12675	.25382

	F7	F8	F9	F10	F11	F12
F7	1.00000					
F8	.60672	1.00000				
F9	.74715	.64292	1.00000			
F10	.49372	.57138	.51362	1.00000		
F11	.76160	.68488	.89191	.75880	1.00000	
F12	.53841	.47888	.48319	.64298	.68875	1.00000
F13	.54411	.49691	.48353	.56021	.66103	.93123
F14	.59992	.61036	.50822	.69296	.72252	.66088
F15	.15814	.07634	.18361	.26103	.33556	.60625
F16	.21545	.34671	.35616	.58347	.37567	.35180
F17	.64480	.67560	.84113	.65984	.88179	.62740
F18	.68576	.31054	.53282	.26101	.52429	.52959
F19	.54815	.45332	.30760	.35063	.39089	.48856
F20	.36421	-.00130	-.16248	.17064	-.06109	.15915
F21	.44316	.13969	.42058	.09116	.40978	.46347
F22	.61558	.46483	.49586	.68831	.70266	.87654
F23	.68522	.46652	.54357	.38108	.58258	.58313
F24	.57206	.55213	.51578	.54414	.63218	.77204
F25	.64392	.48775	.53302	.71496	.71525	.85979
F26	-.30010	-.29680	-.09795	.02785	-.02081	-.03107
F27	.48660	.25703	.08276	-.08091	.06288	.08746

TABLE 4.36: PAN: CORRELATION MATRIX: FACE CONTINUED

	F13	F14	F15	F16	F17	F18
F13	1.00000					
F14	.67463	1.00000				
F15	.69457	.48643	1.00000			
F16	.41844	.32556	.18416	1.00000		
F17	.57268	.55523	.30815	.29396	1.00000	
F18	.52757	.37672	.33857	-.07342	.58585	1.00000
F19	.45761	.21376	.19081	-.00967	.53066	.75326
F20	.18513	.11662	.05662	.15735	.05806	.36776
F21	.45532	.26503	.59051	.01997	.36180	.47944
F22	.75514	.69059	.47115	.20362	.68671	.54178
F23	.63496	.42729	.31537	-.01825	.67510	.83219
F24	.74710	.63059	.60089	.13156	.71240	.75739
F25	.73855	.72073	.47161	.23404	.68903	.54211
F26	-.10522	-.20086	-.18191	-.07499	.14903	.01649
F27	.19541	.23026	.07728	-.21555	.11264	.31910

	F19	F20	F21	F22	F23	F24
F19	1.00000					
F20	.54125	1.00000				
F21	.48394	.12363	1.00000			
F22	.59182	.30762	.57211	1.00000		
F23	.74383	.37862	.33955	.63257	1.00000	
F24	.70147	.27145	.51599	.80794	.78397	1.00000
F25	.56365	.29788	.52131	.98815	.63508	.79750
F26	.06822	-.05460	.19012	.05272	-.15103	.10019
F27	.32268	.52787	.17526	.18191	.42576	.19530

	F25	F26	F27
F25	1.00000		
F26	-.01602	1.00000	
F27	.19394	-.32717	1.00000

TABLE 4.37: GORILLA: CORRELATION MATRIX: FACE

	F1	F2	F3	F4	F5	F6
F1	1.00000					
F2	.82162	1.00000				
F3	.84712	.48942	1.00000			
F4	.53955	.32418	.42222	1.00000		
F5	.85810	.69684	.74387	.40718	1.00000	
F6	.93559	.80558	.81551	.39422	.86411	1.00000
F7	.89910	.74134	.83199	.34892	.83804	.96306
F8	.94495	.82173	.79176	.46575	.83717	.94920
F9	.78136	.69826	.77000	.10761	.69563	.88578
F10	.77180	.66648	.67447	.29182	.58243	.78019
F11	.85463	.74071	.81680	.26039	.69943	.89586
F12	.53245	.35508	.33336	.54367	.55956	.55788
F13	.45686	.25585	.31027	.51609	.49714	.49057
F14	.56830	.43296	.63529	.18401	.40023	.61228
F15	.32665	.36457	.26126	.20122	.29707	.39314
F16	.47796	.17310	.58598	.47042	.49213	.50997
F17	.79972	.72433	.77037	.10453	.66086	.86170
F18	.79023	.51738	.82841	.28695	.72763	.78720
F19	.83785	.61370	.85995	.26553	.75495	.82664
F20	.90435	.74381	.78392	.45066	.86416	.91672
F21	.77827	.65609	.67114	.27355	.75585	.87401
F22	.78963	.74168	.68728	.15502	.74895	.88070
F23	.77278	.53085	.88666	.28331	.70701	.80995
F24	.77649	.68712	.64634	.05828	.81200	.86454
F25	.80199	.74400	.69568	.16337	.77035	.88748
F26	.79809	.63958	.70479	.28824	.62851	.75762
F27	.68944	.65526	.59478	.11064	.67269	.76087

	F7	F8	F9	F10	F11	F12
F7	1.00000					
F8	.87268	1.00000				
F9	.89637	.78355	1.00000			
F10	.83232	.71392	.72797	1.00000		
F11	.91131	.83160	.91448	.90781	1.00000	
F12	.57609	.45066	.35834	.40657	.32395	1.00000
F13	.53109	.36759	.29949	.41882	.29110	.97649
F14	.67408	.53814	.71622	.61075	.67913	.40558
F15	.36471	.32411	.37765	.09381	.28639	.25394
F16	.60959	.44441	.40383	.48298	.45630	.51552
F17	.90880	.77469	.94054	.80358	.92111	.32767
F18	.80824	.70598	.78185	.57626	.71377	.53143
F19	.84456	.78551	.83894	.61113	.79294	.36409
F20	.93120	.88301	.79357	.77628	.81766	.63285
F21	.86561	.75584	.83161	.65792	.74539	.73210
F22	.90022	.79197	.92088	.73265	.85460	.43209
F23	.84755	.74414	.84273	.59903	.76371	.42556
F24	.86284	.78165	.88595	.67535	.80088	.52180
F25	.89606	.79571	.91182	.74665	.84641	.43335
F26	.70675	.72989	.72925	.64737	.79767	.25585
F27	.83478	.65072	.79436	.71287	.80465	.49833

TABLE 4.37: GORILLA: CORRELATION MATRIX: FACE CONTINUED

	F13	F14	F15	F16	F17	F18
F13	1.00000					
F14	.40273	1.00000				
F15	.10080	.16074	1.00000			
F16	.55383	.30459	.12722	1.00000		
F17	.28191	.74073	.35340	.39599	1.00000	
F18	.47311	.76657	.32620	.43222	.77818	1.00000
F19	.30168	.71828	.25800	.50447	.81937	.91284
F20	.57076	.65180	.32569	.57622	.79074	.83634
F21	.69601	.61970	.31163	.47923	.77673	.78310
F22	.35243	.64429	.36594	.45153	.87924	.78127
F23	.38153	.81176	.39197	.53660	.82494	.91566
F24	.45885	.60240	.23837	.34065	.84055	.75988
F25	.36211	.65070	.33356	.48290	.87081	.80704
F26	.16273	.50525	.39929	.14662	.76874	.73911
F27	.45624	.69688	.44099	.39926	.83401	.67612

	F19	F20	F21	F22	F23	F24
F19	1.00000					
F20	.82680	1.00000				
F21	.70528	.82611	1.00000			
F22	.82423	.87755	.78139	1.00000		
F23	.90124	.84050	.74704	.80392	1.00000	
F24	.77128	.81709	.85981	.89708	.72137	1.00000
F25	.85680	.88079	.77565	.99624	.82102	.89157
F26	.73002	.65056	.57981	.69611	.61255	.69291
F27	.68982	.74721	.75232	.75382	.70030	.81017

	F25	F26	F27
F25	1.00000		
F26	.70358	1.00000	
F27	.74196	.61910	1.00000

TABLE 4.38: PONGO: CORRELATION MATRIX: FACE

	F1	F2	F3	F4	F5	F6
F1	1.00000					
F2	.78246	1.00000				
F3	.72489	.36839	1.00000			
F4	.60090	.57421	.52909	1.00000		
F5	.34455	.11898	.39163	.20806	1.00000	
F6	.92885	.80071	.66864	.68916	.39405	1.00000
F7	.90354	.78252	.66715	.53438	.49758	.93327
F8	.96842	.80320	.69628	.64782	.41550	.95525
F9	.79583	.62436	.62981	.53747	.70308	.87024
F10	.67258	.44378	.71989	.54157	.41558	.69314
F11	.79856	.62270	.67955	.61687	.56902	.83672
F12	.75123	.64894	.69136	.68274	.38351	.73514
F13	.72682	.67059	.69531	.69648	.37052	.75952
F14	.40539	.50781	.21537	.52648	.01251	.47217
F15	.52446	.38713	.22582	.09850	-.08215	.35553
F16	-.04186	-.03980	.18957	.06602	.27191	.01192
F17	.83813	.67959	.61180	.49911	.56825	.89293
F18	.80057	.59514	.70108	.41467	.66744	.77644
F19	.89067	.66639	.70997	.40972	.56517	.82636
F20	.83158	.69692	.59169	.36830	.23422	.75645
F21	.83531	.70416	.61588	.64952	.56102	.87757
F22	.90913	.69819	.71649	.60958	.46734	.84428
F23	.76832	.60195	.62463	.58516	.65145	.76187
F24	.70975	.48268	.40110	.40807	.63350	.66986
F25	.90920	.69279	.72762	.60140	.48471	.84895
F26	.82705	.61622	.49300	.41268	.27212	.73768
F27	.70426	.60970	.57182	.45540	.46434	.76219

	F7	F8	F9	F10	F11	F12
F7	1.00000					
F8	.94013	1.00000				
F9	.90379	.85240	1.00000			
F10	.72357	.66123	.74155	1.00000		
F11	.87165	.81736	.91193	.92301	1.00000	
F12	.71711	.77750	.65212	.62487	.69721	1.00000
F13	.75862	.76184	.69963	.68236	.76409	.94220
F14	.44624	.47540	.40534	.24153	.38529	.60115
F15	.41409	.40521	.22738	.41842	.41697	.34705
F16	.11192	.05528	.04343	.05074	.00050	.31091
F17	.95693	.90189	.91682	.71390	.86249	.65869
F18	.91041	.84962	.87908	.76514	.86952	.72676
F19	.91499	.91029	.82676	.65942	.79490	.72857
F20	.79976	.78057	.60002	.65298	.71536	.62484
F21	.84982	.87949	.87695	.77522	.88441	.86009
F22	.84578	.89290	.77953	.72703	.83369	.87200
F23	.85164	.82978	.82600	.76150	.87520	.73346
F24	.68554	.73786	.72474	.43275	.65301	.63357
F25	.86688	.90534	.78932	.75454	.85760	.86238
F26	.74552	.77994	.59934	.64151	.70886	.54576
F27	.83743	.76524	.83636	.75088	.82246	.63851

TABLE 4.38: PONGO: CORRELATION MATRIX: FACE CONTINUED

	F13	F14	F15	F16	F17	F18
F13	1.00000					
F14	.67992	1.00000				
F15	.28090	.09133	1.00000			
F16	.18682	.13568	-.09789	1.00000		
F17	.67920	.40835	.41031	.13647	1.00000	
F18	.71407	.34500	.39842	.26034	.92589	1.00000
F19	.67829	.31500	.47963	.15295	.91107	.95225
F20	.59523	.25812	.72298	-.01700	.76348	.76051
F21	.84511	.52308	.33513	.13607	.83921	.84051
F22	.81276	.46114	.59313	.16990	.82904	.84911
F23	.71606	.38155	.41122	.27062	.87857	.92855
F24	.53837	.34317	.46751	.24569	.72565	.71903
F25	.81407	.43656	.58808	.18093	.84797	.87943
F26	.46188	.17778	.68270	-.07123	.73679	.72427
F27	.68088	.51492	.25637	.17254	.83062	.81170

	F19	F20	F21	F22	F23	F24
F19	1.00000					
F20	.85928	1.00000				
F21	.81230	.67572	1.00000			
F22	.88348	.83161	.88775	1.00000		
F23	.86966	.72931	.84986	.86572	1.00000	
F24	.74173	.56301	.74772	.82155	.78035	1.00000
F25	.90596	.84939	.89290	.99226	.89982	.82178
F26	.82299	.92608	.68084	.80495	.75020	.63533
F27	.74197	.61393	.79600	.74341	.76830	.57095

	F25	F26	F27
F25	1.00000		
F26	.82455	1.00000	
F27	.74882	.58977	1.00000

APPENDIX 5: RESULTS OF CLADISTIC ANALYSES

SECTION 1A: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMINOIDS (see page 298)

i. ALL TREES REQUIRING 156 OR FEWER STEPS (ALL CHARACTERS)

TREE 1: L=154 CI=.760

```
                                                           H.S. M
                                                             *** 1
                       **************************************9
                       *                                     ****2
          ************12                                   H.S. F
          *            *      ***** 3 PA M
        *13            ******10
        * *                   ***** 4 PA F
        * *
*******14 ***** 8 PO F
*       *
*       *        ********* 5 GO M
*       ********11
*                ***** 6 GO F
*
* 7 PO M
```

TREE 2: L=156 CI=.750

```
                                                         H.S. M
                                                             *** 1
                       **************************************9
                       *                                     ****2
          ************13                                 H. S. F
          *            *      ***** 3 PA M
          *            ******10
*********14                   ***** 4 PA F
*         *
*         *         ********* 5 GO M
*         *********11
*         12        ***** 6 GO F
*          *
*          ***** 8 PO F
*
*  7 PO M
```

```
SECTION 1A: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMINOIDS
i. ALL TREES REQUIRING 156 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED


TREE 3: L=154 CI=.760

                                                            H.S. M
                                                               **1
                             **********************************9
                             *                                 ***2
                  **********11                              H.S. F
                  *          *   ***** 3 PA M
               **12          ***10
               *  *              ***** 4 PA F
     *********13  *
     *         *  *** 6 GO F
****14         *
*    *         ****** 5 GO M
*    *
*    **** 8 PO F
*
* 7 PO M


TREE 4: L=156 CI=.750

                                                          H.S. M
                                                               **1
                             **********************************9
                           *10                                 ***2
                           * *                            H.S. F
               ***********11 **** PA F
               *           *
              12           ** 3 PA M
              **
     ********13**** 6 GO F
     *        *
****14        ***** 5 GO M
*    *
*    **** 8 PO F
*
* 7 PO M
```

```
SECTION 1A: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMINOIDS
i. ALL TREES REQUIRING 156 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED


TREE 5: L=154 CI=.760

                                                         H.S. M
                                                              **1
                         *************************************9
                        10                                    ***2
                        **                               H.S. F
               ********11***** 3 PA M
               *        *
      ********13        ** 4 PA F
      *        *
      *        *   ******** 5 GO M
*****14        ***12
*     *            **** 6 GO F
*     *
*     *** 8 PO F
*
* 7 PO M


TREE 6: L=153 CI=.765

                                                          H.S. M
                                                              **1
                          ************************************9
                          *                                   ***2
                 ********12                               H.S. F
                 *        *   ***** 3 PA M
                 *        ***10
       *********13            ***** 4 PA F
       *         *
       *         *   ******** 5 GO M
******14         ***11
*      *             **** 6 GO F
*      *
*      *** 8 PO F
*
* 7 PO M
```

SECTION 1A: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMINOIDS
i. ALL TREES REQUIRING 156 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED

TREE 7: L=152 CI=.770

```
                                                           H.S. M
                                                               **1
                          *************************************9
                      **10                                     ***2
                      *   *                                H.S. F
              *******11   **** 4 PA F
              *       *
      *******13       *** 3 PA M
      *       *
      *       *     ******** 5 GO M
*****14       *****12
*     *             *** 6 GO F
*     *
*     **** 8 PO F
*
* 7 PO M
```

TREE 8: L=155 CI=.755

```
                                                           H.S. M
                                                               **1
                              *********************************9
                              *                                ***2
                   **********11                            H.S. F
                   *          *   ***** 3 PA M
                 *12          ***10
                 * *              ***** 4 PA F
     **********13  *
     *           * ******* 5 GO M
****14           *
*    *           *** 6 GO F
*    *
*    **** 8 PO F
*
* 7 PO M
```

SECTION 1A: NON-VARIABLE TRAITS: SEXES OF EXTANT HOMINOIDS
i. ALL TREES REQUIRING 156 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED

TREE 9: L=156 CI=.750

```
                                                          H.S.M
                                                             ***1
                     ****************************************9
                     *                                       ****2
                     *                                    H.S. F
        ************13       ***** 3 PA M
        *            *   ***10
        *            *   *   ****** 4 PA F
        *            ****12
*******14                *         ********* 5 GO M
*       *                *********11
*       *                          **** 6 GO F
*       *
*       *** 8 PO F
*
* 7 PO M
```

ii. SHORTEST TREE WITH CHARACTERS M9 AND B2 DELETED

L=143 CI=.790

```
                                                          H.S. M
                                                              **1
                        **************************************9
                      *10                                     ***2
                      * *                                 H.S. F
            *********11 ***** 4 PA F
            *         *
    *******13         ** 3 PA M
    *       *
    *       *    ******** 5 GO M
***14       ****12
*   *            *** 6 GO F
*   *
*   ***** 7 PO M
*
* 8 PO F
```

SECTION 1B: VARIABLE TRAITS: SEXES OF HOMINOIDS (See page 294)

i. ALL TREES REQUIRING 128 OR FEWER STEPS (ALL CHARACTERS)

TREE 1: L=128 CI=.727

```
                                                      H.S. M
                                                         **1
                           ******************************9
                           *                             *********2
                           *                              H.S. F
        ******************13                         **** 3 PA M
        *                  *                 ******10
        *                  *        ********11       ******* 4 PA F
        *                  *        *        *
*******14                  ********12        ***** 6 GO F
*       *                           *
*       *                           ******** 5 GO M
*       *
*       ***** 8 PO F
*
* 7 PO M
```

TREE 2: L=128 CI=.727

```
                                                         H.S. M
                                                         ** 1
                      ***********************************9
                      *                                  *********2
                      *                                  H.S. F
         ************13          *** 3 PA M
         *            *       **10
         *            *       *  ******* 4 PA F
         *            *******12
********14                    *    **************** 5 GO M
*        *                    ****11
*        *                         ***** 6 GO F
*        *
*        **** 8 PO F
*
* 7 PO M
```

SECTION 1B: VARIABLE TRAITS: SEXES OF HOMINOIDS
i. ALL TREES REQUIRING 128 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED

TREE 3: L=127 CI=.732

```
                                                        H.S. M
                                                        ** 1
                      **********************************9
                      *                                 *********2
                      *                                 H.S. F
         ************13          *** 3 PA M
         *            *      ***11
         *            *      *   *      **************** 5 GO M
         *            ******12   ******10
********14                   *          ***** 6 GO F
*        *                   *
*        *                   **** 4 PA F
*        *
*        **** 8 PO F
*
* 7 PO M
```

TREE 4: L=126 CI=.738

```
                                                            H.S. M
                                                            ****1
                               *****************************9
                     *********11                            *****2
                     *         *                            H.S. F
                   *12         **** 6 GO M
                   * *
      ************13 **** 6 GO F
      *            *
      *            *  **** 3 PA M
*****14            **10
*     *               ****** 4 PA F
*     *
*     ***** 8 PO F
*
* 7 PO M
```

SECTION 1B: VARIABLE TRAITS: SEXES OF HOMINOIDS
i. ALL TREES REQUIRING 128 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED

TREE 5: L=126 CI=.732

```
                                                            H.S. M
                                                            ****1
                                 ***************************9
                        ********10                          *****2
                        *        *                          H.S. F
                   ****11        **** 5 GO M
                   *    *
                 *12    ***** 6 GO F
                 * *
    ************13 ** 3 PA M
***14            *
*   *            *** 4 PA F
*   ****** 8 PO F
*
* 7 PO M
```

TREE 6: L=127 XI=.732

```
                                                          H.S. M
                                                            ****1
                               *****************************9
                     *********11                            *****2
                     *         *                          H.S. F
                     *         ****** 5 GO M
       *************13
       *             *    *** 3 PA M
       *             ****10
******14             12   ****** 4 PA F
*      *              *
*      *              ***** 6 GO F
*      *
*      **** 8 PO F
*
* 7 PO M
```

SECTION 1B: VARIABLE TRAITS: SEXES OF HOMINOIDS
i. ALL TREES REQUIRING 128 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED

TREE 7: L=127 CI=.732

```
                                                          H.S. M
                                                            ****1
                                     ***********************9
                          **********10                      *****2
                          *          *                    H.S. F
                      ***11          ******** 5 GO M
                      *   *
                 ****12   ** 4 PA F
                 *    *
      **********13    *** 3 PA M
      *          *
*****14          **** 6 GO F
*     *
*     **** 8 PO F
*
* 7 PO M
```

TREE 8: L=125 CI=.744

```
                                                           H.S. M
                                                            ****1
                                 ***************************9
                       *********11                          *****2
                       *         *                         H.S. F
                   ***12         ******** 5 GO M
                   *   *
                   *   *  ** 3 PA M
      ************13   **10
      *            *      ****** 4 PA F
*****14            *
*     *            **** 6 GO F
*     *
*     ***** 8 PO F
*
* 7 PO M
```

SECTION 1B: VARIABLE TRAITS: SEXES OF HOMINOIDS
i. ALL TREES REQUIRING 128 OR FEWER STEPS (ALL CHARACTERS)
CONTINUED

TREE 9: L=126 CI=.738

```
                                                           H.S. M
                                                            ****1
                                   *************************9
                        **********10                        *****2
                        *          *                       H.S. F
                      *11          ******** 5 GO M
                      * *
                  ***12 ** 3 PA M
                  *   *
      ***********13   ****** 4 PA F
      *           *
*****14           **** 6 GO F
*     *
*     ***** 8 PO F
*
* 7 PO M
```

TREE 10: L=128 CI=.727

```
                                                          H.S. M
                                                            ****1
                                 ***************************9
                        ********10                          *****2
                        *        *                        H.S. F
                       11        ********* 5 GO M
                       **
                    **12**** 3 PA M
                    *  *
      *************13  ******* 6 GO F
      *             *
*****14             **** 4 PA F
*     *
*     ***** 8 PO F
*
* 7 PO M
```

SECTION 1B: VARIABLE TRAITS: SEXES OF HOMINOIDS

ii. SHORTEST TREE WITH CHARACTERS V14 V15 F5 DELETED
L=95 CI=.832

```
                                                       H.S. M
                                                          *** 1
                               ***************************9
                    **********11                          ******2
                    *          *                       H.S. F
               ****12          ******* 5 GO M
               *    *
               *    * *** 3 PA M
     *********13    *10
     *         *      ***** 4 PA F
****14         *
*    *         ** 6 GO F
*    *
*    ******* 7 PO M
*
* 8 PO F
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT (see page 299)

i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)

TREE 1: L=178 CI=.646

```
* 1 OUTGROUP                                                 H.S.
*                                                                2
*                                                *****************
*                                      **********9
*                                *****10         ******* 8 H.ER
*                                *     *
*                     **********11     * 7 H.HAB
*                     *          *
*             *******12          ******* 5 A.ROB
*             *       *
*       *****13       ***** 6 A.BOIS
*       *     *
*******14     ****** 3 A.AFAR
        *
        ******* 4 A.AFRIC
```

TREE 2: L=178 CI=.646

```
* 1 OUTGROUP
*                                                             H.S.
*                                    ****************************2
*                       *************9
*                 *****11            ************ 8 H.ER
*                 *     *
*                 *     ******* 4 A.AFRIC
*****************14
                  *              **************** 3 A.AFAR
                  *       ******10
                  *       *      ************ 6 A.BOIS
                  *******13
                          *            *************** 5 A.ROB
                          ************12
                                       ******* 7 H.HAB
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 3: L=176 CI=.653

```
* 1 OUTGROUP
*                                                           H.S.
*                                       *************************2
*                               ********9
*                               *       ********** 8 H.ER
*                      ********12
*                      *        *        *******************  5
*                      *        ********11                   A.ROB
*               ******13                 * 7 H.HAB
*               *      *
*               *      *        ********** 3 A.AFAR
***************14      ********10
                *               *************** 6 A.BOIS
                *
                ****** 4 A.AFRIC
```

TREE 4: L=177 CI=.650

```
* 1 OUTGROUP
*                                                           H.S.
*                                     ***************************2
*                            *********9
*                            *        *********** 8 H.ER
*                  *********13
*                  *         *         ******************** 5
*                  *         *********12                   A.ROB
*****************14                    * 7 H.HAB
                   *
                   *           ********** 3 A.AFAR
                   * *********10
                   *11         ****************** 6 A.BOIS
                     *
                     *********4 A.AFRIC
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 5: L=178 CI=.646

```
* 1 OUTGROUP
*
*                                                          H.S.
*                                      **************************2
*                            **********9
*                       ****11         *********** 8 H.ER
*                       *    *
*                ******13    ********* 4 A.AFRIC
*                *      *
*                *      *             ***************** 5 A.ROB
****************14      *************12
                 *                    *** 7 H.HAB
                 *
                 *    ************ 3 A.AFAR
                 ****10
                      *************** 6 A.BOIS
```

TREE 6: L=175 CI=.657

```
* 1 OUTGROUP
*
*                                                           H.S.
*                                       *************************2
*                                *******9
*                                *      *********** 8 H.ER
*                    ***********12
*                    *           *       ******************* 5
*              *****13           *******11                A.ROB
*              *     *                   * 7 H.HAB
*              *     *
**************14     ******* 4 A.AFRIC
               *
               *     ******** 3 A.AFAR
               *****10
                     **************** 6 A.BOIS
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 7: L=178 CI=.646

```
* 1 OUTGROUP
*
*                                  ********************** 2 H.S.
*                              ***11                        A.ROB
*                              *   *              ****************5
*                 ************12   **************10
*                 *            *                  * 7 H.HAB
*            ****13            *
*            *    *            ***** 8 H.ER
*            *    *
************14    ******* 4 A.AFRIC
             *
             *    ******** 3 A.AFAR
             *****9
                  *************** 6 A.BOIS
```

TREE 8: L=176 CI=.653

```
* 1 OUTGROUP
*
*                                                         H.S.
*                                      **************************2
*                         *************9
*                   *****11            ********** 8 H.ER
*                   *     *
*               ***13     ******* 4 A.AFRIC
*               *   *
*               *   *      *********** 3 A.AFAR
***************14   ******10
                *          **************** 6 A.BOIS
                *
                *             ************** 5 A.ROB
                *************12
                              ***** 7 H.HAB
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 9: L=177 CI=.650

```
* 1 OUTGROUP
*                                                            H.S.
*                                     ****************************2
*                      ***************9
*              ******10               ************ 8 H.ER
*              *       *
*              *       ***** 4 A.AFRIC
**************14
               *
               *                                             A.ROB
               ********13                              ***********5
                        *          ******************11
                        **********12                   **********7
                                   *                        H.HAB
                                   ********* 6 A.BOIS
```

TREE 10: L=178 CI=.646

```
* 1 OUTGROUP
*                                                          H.S.
*                                           ***********************2
*                                 **********9
*                         ******11          ********* H.ER
*                         *       *
*                ********12       ***** 7 H.HAB
*                *        *
*                *        *           ************ 5 A.ROB
*            ***13        **********10
*            *   *                    ******** 6 A.BOIS
************14   *
             *   *********** 3 A.AFAR
             *
             ****** 4 A.AFRIC
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 11: L=178 CI=.646

```
* 1 OUTGROUP
*                                                        H.S.
*                                 ************************** 2
*                           ******9
*                           *     ******* 8 H.ER
*                   *******12                             A.ROB
*                   *       *                       ********** 5
*                   *       *        **************10
*               ***13       ********11              *************6
*               *   *                *                     A.BOIS
*               *   *                **** 7 H.HAB
***************14   *
                *   ************* 3 A.AFAR
                *
                **** 4 A.AFRIC
```

TREE 12: L=178 CI=.646

```
* 1 OUTGROUP
*                                                         H.S.
*                                      **************************2
*                         *************9
*                   *****10            ********** 8 H.ER
*                   *     *
*                   *     ******* 4 A.AFRIC
*               ***13
*               *   *                     *********** 5 A.ROB
*               *   *        ************11
***************14   ********12            ********** 7 H.HAB
                *            *
                *            ************** 6 A.BOIS
                *
                ************* 3 A.AFAR
```

```
SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED


TREE 13: L=178 CI=.646


* 1 OUTGROUP
*                                                          H.S.
*                                        ************************2
*                                ********9
*                     **********11       **********
*                     *          *
*                  **12          ********** 7 H.HAB
*                  *  *
*             ****13  ******** 4 A.AFRIC
*             *    *
*************14    ************ 3 A.AFAR
              *
              *             ***************** 5 A.ROB
              *************10
                            ***** 6 A.BOIS


TREE 14: L=178 CI=.646


* 1 OUTGROUP
*                                                          H.S.
*                                      **************************2
*                              ********9
*                      *******12       ********** 8 H.ER
*                      *       *
*               ******13       *********** 7 H.HAB
*               *      *
*               *      *   *************** 3 A.AFAR
***************14      ***10
                *          ********* 4 A.AFRIC
                *
                *            ***************** 5 A.ROB
                ************11
                             ******* 6 A.BOIS
```

```
SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
i. ALL TREES OF 178 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED


TREE 15: L=178 CI=.646


* 1 OUTGROUP
*                                                         H.S.
*                                      **************************2
*                        **************9
*                    ***10             ********** 8 H.ER
*                    *   *
*               ****11   ****** 4 A.AFRIC
*               *    *
*               *    ************* 3 A.AFAR
***************14
                *                       *********** 5 A.ROB
                *        **************12
                ********13              ********** 7 H.HAB
                         *
                         ************* 6 A.BOIS
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT

ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR) (see page 303)

TREE 1: L=181 CI=.657

```
* 1 OUTGROUP
*                                                          H.S.
*                                           **********************2
*                                     ******9
*                                     *     ********* 8 H.ER
*                           *********11
*                           *         *      **************** 5
*                     *****12         ******10            A.ROB
*                     *     *                 * 7 H.HAB
*                ****13     *
*                *    *     ******* 4 A.AFRIC
****************14    *
                 *    ******* 3 A.AFAR
                 *
                 ************ 6 A.BOIS
```

TREE 2: L=180 CI=.661

```
* 1 OUTGROUP
*                                                         H.S.
*                                        *************************2
*                                ********9
*                                *       ********** 8 H.ER
*                        *******12
*                        *       *        ****************** 5
*                        *       ********11                A.ROB
*                  *****13                * 7 H.HAB
*                  *     *
*                  *     *       ********** 3 A.AFAR
******************14     *******10
                   *             *************** 6 A.BOIS
                   *
                   ***** 4 A.AFRIC
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 3: L=179 CI=.665

```
* 1 OUTGROUP
*                                                         H.S.
*                                        ************************2
*                                 *******9
*                                 *      ********** 8 H.ER
*                      **********12
*                      *          *       ****************** 5
*                *****13          *******11                A.ROB
*                *     *                  * 7 H.HAB
*                *     *
****************14     ****** 4 A.AFRIC
                 *
                 *     ******** 3 A.AFAR
                 *****10
                       *************** 6 A.BOIS
```

TREE 4: L=181 CI=.657

```
* 1 OUTGROUP
*                                                          H.S.
*                                         ***********************2
*                                  *******9
*                         ********11      ********* 8 H.ER
*                         *        *
*                   *****12        ********* 7 H.HAB
*                   *     *
*            ******13     ******** 4 A.AFRIC
*            *      *
*            *      *   ********** 3 A.AFAR
************14      ***10
             *          ************* 6 A.BOIS
             *
             **************** 5 A.ROB
```

```
SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 5: L=179 CI=.665


* 1 OUTGROUP
*                                                        H.S.
*                                       *************************2
*                           ************9
*                     *****11           ********** 8 H.ER
*                     *     *
*                ****13     ******* 4 A.AFRIC
*                *    *
*                *    *       ********** 3 A.AFAR
****************14    *******10
                 *            *************** 6 A.BOIS
                 *
                 *            ************** 5 A.ROB
                 ************12
                              ***** 7 H.HAB


TREE 6: L=181 CI=.657


* 1 OUTGROUP
*                                                           H.S.
*                                     **************************2
*                       **************9
*                 *****10             *********** 8 H.ER
*                 *     *
*                 *     ***** 4 A.AFRIC
*****************14
                  *       ******** 3 A.AFAR
                  *       *
                  *******13                       *********** 5
                          *         *************11        A.ROB
                          *********12             ********** 7
                                    *                     H.HAB
                                    ******** 6 A.BOIS
```

```
SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 7: L=180 CI=.661


* 1 OUTGROUP
*                                                          H.S.
*                                         ***********************2
*                                  *******9
*                       **********11      ********* 8 H.ER
*                       *          *
*                    **12          ********* 7 H.HAB
*                    *  *
*              *****13  ******** 4 A.AFRIC
*              *     *
**************14     *********** 3 A.AFAR
               *
               *          ***************** 5 A.ROB
               **********10
                          ****** 6 A.BOIS


TREE 8: L=180 CI=.661


* 1 OUTGROUP
*                                                         H.S.
*                                       *************************2
*                                *******9
*                        *******12      ********** 8 H.ER
*                        *       *
*               ********13       ********** 7 H.HAB
*               *        *
*               *        *   ************** 3 A.AFAR
***************14        ***10
                *            ********* 4 A.AFRIC
                *
                *          ***************** 5 A.ROB
                **********11
                           ******** 6 A.BOIS
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 9: L=181 CI=.657

```
* 1 OUTGROUP
*                                                           H.S.
*                                       ************************2
*                                 ******9
*                      **********11     ********** 8 H.ER
*                      *          *
*                    *12          *********** 7 H.HAB
*                    * *
*             ******13 ************* 3 A.AFAR
*             *      *
*************14      ******** 4 A.AFRIC
              *
              *            ***************** 5 A.ROB
              ************10
                           ***** 6 A.BOIS
```

TREE 10: L= 181 CI=.657

```
* 1 OUTGROUP
*                                                           H.S.
*                                      **************************2
*                                 *****9
*                                 *    ****** 8 H.ER
*                        ********12
*                        *        *    ************ 3 A.AFAR
*                *******13        ****10
*                *       *             ********* 4 A.AFRIC
*                *       *
****************14       ****** 7 H.HAB
                 *
                 *      ********** 5 A.ROB
                 ******11
                        ********** 6 A.BOIS
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 11: L=180 CI=.661

```
* 1 OUTGROUP
*
*                                                           H.S.
*                                       *************************2
*                          *************9
*                      ***10            ********** 8 H.ER
*                      *   *
*               ******11   ****** 4 A.AFRIC
*               *      *
*               *      ************ 3 A.AFAR
***************14
                *                     *********** 5 A.ROB
                *       *************12
                *******13             ********** 7 H.HAB
                        *
                        ************ 6 A.BOIS
```

TREE 12: L=181 CI=.657

```
* 1 OUTGROUP
*                                                           H.S.
*                                     ***************************2
*                            *********9
*                     ******10        **** 8 H.ER
*                     *      *
*                ****11      ******** 3 A.AFAR
*                *    *
*                *    ******* 4 A.AFRIC
****************14
                 *                 ********* 5 A.ROB
                 *      **********12
                 ******13          ********* H.HAB
                        *
                        ************ 6 A.BOIS
```

SECTION 2A: NON-VARIABLE TRAITS: OWN CONSTANT
ii. ALL TREES OF 180 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 13: L=181 CI=.657

```
* 1 OUTGROUP
*                                                            H.S.
*                                         ***********************2
*                                    *****9
*                                    *    ***** 8 H.ER
*                           ********11
*                           *        *    *********** 3 A.AFAR
*                    ******12        ****10
*                    *      *             ******** 4 A.AFRIC
*              *****13      *
*              *     *      **** 7 H.HAB
**************14     *
               *     ******** 5 A.ROB
               *
               ************ 6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED (See pg. 306)

i. ALL TREES OF 129 STEPS OR LESS (COMBINED ANCESTOR)

TREE 1: L=128 CI=.734

```
* 1 OUTGROUP
*                                                          H.S.
*                                       *************************2
*                             **********9
*                             *         ******** 8 H.ER
*                    ********11
*                    *        *      *************** 5 A.ROB
*                ***12        ******10
*                *   *               * 7 H.HAB
*             **13   *
*             *  *   ***** 4 A.AFRIC
*************14  *
              *  *********** 3 A.AFAR
              *
              *************** 6 A.BOIS
```

TREE 2: L=129 CI=.729

```
* 1 OUTGROUP
*                                                         H.S.
*                                         ***********************2
*                            *************9
*                            *            ******* 8 H.ER
*                  *********11
*                  *         *   ************** 5 A.ROB
*              ***12         ***10
*              *   *             * 7 H.HAB
*           **13   *
*           *  *   ************ 6 A.BOIS
***********14  *
            *  *********** 3 A.AFAR
            *
            ******** 4 A.AFRIC
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
i. ALL TREES OF 129 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 3: L=127 CI=.740

```
* 1 OUTGROUP
*                                                           H.S.
*                                       *************************2
*                             **********9
*                             *         ******** 8 H.ER
*                     *******11
*                     *       *      *************** 5 A.ROB
*              ******12       ******10
*              *      *              * 7 H.HAB
*            *13      *
*            * *      ****** 4 A.AFRIC
************14 *
             * ************** 6 A.BOIS
             *
             *********** 3 A.AFAR
```

TREE 4: L=129 CI=.729

```
* 1 OUTGROUP
*                                                        H.S.
*                                      **************************2
*                           ***********9
*                           *          ******** 8 H.ER
*                  ********12
*                  *        *      **************** 5 A.ROB
*                  *        ******11
*               **13               * 7 H.HAB
*               *  *
*               *  *     ************* 3 A.AFAR
***************14  *****10
                *        ************** 6 A.BOIS
                *
                ****** 4 A.AFRIC
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
i. ALL TREES OF 129 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 5: L=129 CI=.729

```
* 1 OUTGROUP
*                                                            H.S.
*                                    ****************************2
*                         ***********9
*                         *          ********* 8 H.ER
*                ********13
*                *        *      ***************** 5 A.ROB
*                *        ******12
****************14               * 7 H.HAB
                 *
                 *        ************ 3 A.AFAR
                 * ******10
                 *11      **************** 6 A.BOIS
                   *
                   ********* 4 A.AFRIC
```

TREE 6: L=127 CI=.740

```
* 1 OUTGROUP
*                                                           H.S.
*                                       *************************2
*                            ***********9
*                            *          ******** 8 H.ER
*                  *********12
*                  *         *      *************** 5 A.ROB
*             ****13         ******11
*             *    *                * 7 H.HAB
*             *    *
*************14    ****** 4 A.AFRIC
              *
              * *********** 3 A.AFAR
              *10
                ************** 6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
i. ALL TREES OF 129 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 7: L=129 CI=.729

```
* 1 OUTGROUP
*                                                           H.S.
*                                    ****************************2
*                     ***************9
*                ****11              ******* 8 H.ER
*                *    *
*           ****13    ***** 4 A.AFRIC
*           *    *
*           *    *   ************ 3 A.AFAR
***********14    ***10
            *        *************** 6 A.BOIS
            *
            *             ************** 5 A.ROB
            *************12
                          *** 7 H.HAB
```

TREE 8: L=129 CI=.729

```
* 1 OUTGROUP
*                                                            H.S.
*                                   *****************************2
*                   ****************9
*             *****10               ******** 8 H.ER
*             *     *
*             *     ****** 4 A.AFRIC
*************14
              *  ************* 3 A.AFAR
              *  *
              **13                        ********** 5 A.ROB
                 *       ****************11
                 *******12                ******* 7 H.HAB
                         *
                         ******** 6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
i. ALL TREES OF 129 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 9: L=129 CI=.729

```
* 1 OUTGROUP
*                                                           H.S.
*                                    ****************************2
*                     ***************9
*                ****10              ******* 8 H.ER
*                *    *
*                *    ***** 4 A.AFRIC
*            ***13
*            *   *                    ********** 5 A.ROB
*            *   *       ************11
************14   *******12            ******* 7 H.HAB
             *           *
             *           *********** 6 A.BOIS
             *
             ************* 3 A.AFAR
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED

ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR) (see page 310)

TREE 1: L=130 CI=.738

```
* 1 OUTGROUP
*                                                            H.S.
*                                      **************************2
*                              *********9
*                              *       ******** 8 H.ER
*                    *********11
*                    *         *       **************** 5 A.ROB
*                   12         *******10
*                   **                 * H.HAB
*             *****13*
*             *     ************** 3 A.AFAR
*************14     *
              *     ******* 4 A.AFRIC
              *
              **************** 6 A.BOIS
```

TREE 2: L=130 CI=.738

```
* 1 OUTGROUP
*                                                           H.S.
*                                      **************************2
*                             *********9
*                             *        ******** 8 H.ER
*                    ********12
*                    *        *      **************** 5 A.ROB
*                    *        ******11
*              *****13              * H.HAB
*              *     *
*              *     *************** 3 A.AFAR
**************14     10
               *      ******* 4 A.AFRIC
               *
               *************** 6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 3: L=128 CI=.750

```
* 1 OUTGROUP
*                                                           H.S.
*                                        ************************2
*                              **********9
*                              *         ******* 8 H.ER
*                    *********11
*                    *         *     *************** 5 A.ROB
*                 **12         *****10
*                 *  *               * 7 H.HAB
*             ***13  *
*             *   *  ****** 4 A.AFRIC
*************14   *
              *   *********** 3 A.AFAR
              *
              ************** 6 A.BOIS
```

TREE 4: L=130 CI=.738

```
* 1 OUTGROUP
*                                                           H.S.
*                                         ***********************2
*                             ************9
*                             *           ******* 8 H.ER
*                  **********11
*                  *          *  ************** 5 A.ROB
*               **12          **10
*               *  *             * 7 H.HAB
*            **13  *
*            *  *  ************* 6 A.BOIS
************14  *
             *  ********** 3 A.AFAR
             *
             ******* 4 A.AFRIC
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

```
TREE 5: L=128 CI=.750


* 1 OUTGROUP
*                                                           H.S.
*                                        ************************2
*                              **********9
*                              *         ******* 8 H.ER
*                     ********11
*                     *        *     *************** 5 A.ROB
*               *****12        *****10
*               *     *              * 7 H.HAB
*             *13     *
*             * *     ******* 4 A.AFRIC
*************14 *
              * ************** 6 A.BOIS
              *
              ********** 3 A.AFAR


TREE 6: L=130 CI=.738


* 1 OUTGROUP
*                                                          H.S.
*                                      **************************2
*                            **********9
*                            *         ******** 8 H.ER
*                   ********12
*                   *        *     **************** 5 A.ROB
*                   *        *****11
*                **13              * 7 H.HAB
*                *  *
*                *  *     ************ 3 A.AFAR
****************14  *****10
                 *        ************* 6 A.BOIS
                 *
                 ****** 4 A.AFRIC
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 7: L=130 CI=.738

```
* 1 OUTGROUP
*                                                          H.S.
*                                     ***************************2
*                         ************9
*                         *           ******** 8 H.ER
*                 *******13
*                 *       *       **************** 5 A.ROB
*                 *       *******12
*****************14               * 7 H.HAB
                  *
                  *       ************* 3 A.AFAR
                  * *****10
                  *11     **************** 6 A.BOIS
                    *
                    ******** 4 A.AFRIC
```

TREE 8: L=128 CI=.750

```
* 1 OUTGROUP
*                                                          H.S.
*                                       *************************2
*                             **********9
*                             *         ******** 8 H.ER
*                   *********12
*                   *         *     **************** 5 A.ROB
*             *****13         *****11
*             *     *               * 7 H.HAB
*             *     *
*************14     ****** 4 A.AFRIC
              *
              * ************ 3 A.AFAR
              *10
                ***************6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 9: L=130 CI=.738

```
* 1 OUTGROUP
*                                                          H.S.
*                                     ***************************2
*                     ****************9
*                ****11               ******* 8 H.ER
*                *    *
*            ***13    ***** 4 A.AFRIC
*            *   *
*            *   *   ************* 3 A.AFAR
************14   ***10
             *       **************** 6 A.BOIS
             *
             *            *************** 5 A.ROB
             ************12
                          *** 7 H.HAB
```

TREE 10: L=130 CI=.738

```
* 1 OUTGROUP
*                                                         H.S.
*                                    ****************************2
*                    ****************9
*              *****10               ******* 8 H.ER
*              *     *
*              *     ***** 4 A.AFRIC
**************14
               *  ************ 3 A.AFAR
               *  *
               **13                       ********** 5 A.ROB
                  *      ****************11
                  ******12                ******* 7 H.HAB
                         *
                         ********* 6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 11: L=130 CI=.738

```
* 1 OUTGROUP
*                                                         H.S.
*                                     ***************************2
*                     *****************9
*                ****10               ******* 8 H.ER
*                *    *
*                *    ***** 4 A.AFRIC
*             **13
*             *  *                     ********** 5 A.ROB
*             *  *       *************11
*************14  *******12             ******* 7 H.HAB
              *          *
              *          ************ 6 A.BOIS
              *
              ************ 3 A.AFAR
```

TREE 12: L=130 CI=.738

```
* 1 OUTGROUP
*                                                         H.S.
*                                     ***************************2
*                      ***************9
*                  ***10              ******* 8 H.ER
*                  *   *
*             ****11   ****** 4 A.AFRIC
*             *    *
*             *    ************ 3 A.AFAR
*************14
              *                      ********** 5 A.ROB
              *      ***************12
              ******13               ******* 7 H.HAB
                     *
                     ********* 6 A.BOIS
```

SECTION 2B: NON-VARIABLE TRAITS: RECODED
ii. ALL TREES OF 130 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 13: L=130 CI=.738

```
* 1 OUTGROUP
*                                                          H.S.
*                                       ************************2
*                            ***********9
*                        ***10          ****** 8 H.ER
*                        *   *
*                ********11   ***** 4 A.AFRIC
*                *       *
*           ****13       ********* 3 A.AFAR
*           *    *
***********14    ********* 6 A.BOIS
            *
            *         *********** 5 A.ROB
            *********12
                      **** 7 H.HAB
```

SECTION 3: VARIABLE TRAITS (see page 312)

i. ALL TREES OF 184 STEPS OR LESS (COMBINED ANCESTOR)

TREE 1: L=182 CI=.610

```
* 1 OUTGROUP
*                                                           H.S.
*                                                ****************2
*                                        ********9
*                                 ******11       ******* 8 H.ER
*                                 *      *
*                          ******12      ** 7 H.HAB
*                          *      *
*                       **13      ****** 4 A.AFRIC
*                       *  *
***********************14  ******* 6 A.BOIS
                        *
                        *   ************ 3 A.AFAR
                        ***10
                            **** 5 A.ROB
```

TREE 2: L=184 CI=.603

```
* 1 OUTGROUP
*                                                           H.S.
*                                                ****************2
*                                       *********9
*                                  ****11        ******* 8 H.ER
*                                  *    *
*                           ******12    ** 7 H.HAB
*                           *      *
*                         *13      ******* 4 A.AFRIC
*                         * *
*                         * *   ************ 3 A.AFAR
*************************14 ***10
                          *     **** 5 A.ROB
                          *
                          ******* 6 A.BOIS
```

SECTION 3: VARIABLE TRAITS
i. ALL TREES OF 184 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 3: L=184 CI=.603

```
* 1 OUTGROUP
*                                                           H.S.
*                                              ******************2
*                                      ********9
*                                 ****12       ******** 8 H.ER
*                                 *    *
*                                 *    ** 7 H.HAB
*                           *****13
*                           *     *            ************ 3
*                           *     *       ****10         A.AFAR
***************************14     *******11    ****** 5 A.ROB
                            *             *
                            *             ********* 6 A.BOIS
                            *
                            **** 4 A.AFRIC
```

TREE 4: L=183 CI=.607

```
* 1 OUTGROUP
*                                                           H.S.
*                                              ******************2
*                                      ********9
*                                 ****11       ******** 8 H.ER
*                                 *    *
*                             ***12    *** 7 H.HAB
*                             *   *
*                       *****13   ******** 5 A.ROB
*                       *     *
***********************14     **** 4 A.AFRIC
                        *
                        *   ***************** 3 A.AFAR
                        ***10
                            ********* 6 A.BOIS
```

SECTION 3: VARIABLE TRAITS
i. ALL TREES OF 184 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 5: L=184 CI=.603

```
* 1 OUTGROUP
*                                                         H.S.
*                                              ******************2
*                                    *********9
*                                ****12        ******** 8 H.ER
*                                *    *
*                           ****13    ** 7 H.HAB
*                           *    *
*                           *    ******** 4 A.AFRIC
**************************14
                            *      ************** 3 A.AFAR
                            *    *10
                            ****11 ************ 6 A.BOIS
                                 *
                                 **** 5 A.ROB
```

TREE 6: L=180 CI=.617

```
* 1 OUTGROUP
*                                                          H.S.
*                                              ******************2
*                                    *********9
*                              ******12        ******** 8 H.ER
*                              *      *
*                         ****13      ** 7 H.HAB
*                         *    *
*                         *    ****** 4 A.AFRIC
************************14
                          *         ************ 3 A.AFAR
                          *   *****10
                          ***11     ****** 5 A.ROB
                              *
                              ******* 6 A.BOIS
```

```
SECTION 3: VARIABLE TRAITS
i. ALL TREES OF 184 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED


TREE 7: L=184 CI=.603


* 1 OUTGROUP
*                                                          H.S.
*                                              ******************2
*                                     *********9
*                              ******12        ********* 8 H.ER
*                              *      *
*                         ****13      ** 7 H.HAB
*                         *    *
*************************14    ******** 4 A.AFRIC
                          *
                          *      ************ 3 A.AFAR
                          ******11
                                 *  ****** 5 A.ROB
                                 **10
                                    *********** 6 A.BOIS


TREE 8 L=184 CI=.603


* 1 OUTGROUP                                               H.S.
*                                             *******************2
*                                   **********9
*                              ****13         ******** 8 H.ER
*                              *    *
*                              *    ** 7 H.HAB
*                              *
******************************14                   *************3
                               *            ******10        A.AFAR
                               *  *********11      ****** 5 A.ROB
                               *  *         *
                               **12         ******* 6 A.BOIS
                                  *
                                  ****** 4 A.AFRIC
```

SECTION 3: VARIABLE TRAITS
i. ALL TREES OF 184 STEPS OR LESS (COMBINED ANCESTOR)
CONTINUED

TREE 9: L=183 CI=.607

```
* 1 OUTGROUP
*
*                      ********* 2 H.S.
*                      *                                   A.AFAR
*                      *                               **********3
*                      *                          *****9
*                      *                  *******10    ***** 5
**********************14                  *       *      A.ROB
                       *             ****11       ***** 6 A.BOIS
                       *             *    *
                       *      ******12    ***** 4 A.AFRIC
                       *      *      *
                       ******13      **** 7 H.HAB
                              *
                              ***** 8 H.ER
```

SECTION 3: VARIABLE TRAITS

ii. ALL TREES OF 184 STEPS OR LESS (NEW ANCESTOR) (see page 316)

TREE 1: L=183 CI=.607

```
* 1 OUTGROUP
*                                                            H.S.
*                                                ****************2
*                                        ********9
*                                 ******11       ******* 8 H.ER
*                                 *      *
*                          ******12      ** 7 H.HAB
*                          *      *
*                        *13      ****** 4 A.AFRIC
*                        * *
************************14 ******* 6 A.BOIS
                         *
                         *   *********** 3 A.AFAR
                         ***10
                             **** 5 A.ROB
```

TREE 2: L=184 CI=.603

```
* 1 OUTGROUP
*                                                        H.S.
*                                              ******************2
*                                    **********9
*                                ***12         ******* 8 H.ER
*                                *   *
*                                *   *** 7 H.HAB
*                           ****13
*                           *    *            ************** 3
*                           *    *         **10          A.AFAR
***************************14    *********11  ************ 6
                            *              *            A.BOIS
                            *              **** 5 A.ROB
                            *
                            **** 4 A.AFRIC
```

SECTION 3: VARIABLE TRAITS
ii. ALL TREES OF 184 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 3: L=183 CI=.607

```
* 1 OUTGROUP
*                                                          H.S.
*                                              *******************2
*                                     *********9
*                                 ***12        ******** 8 H.ER
*                                 *   *
*                                 *   *** 7 H.HAB
*                           *****13
*                           *     *            ************ 3
*                           *     *       ****10        A.AFAR
***************************14     *******11    ******
                            *             *
                            *             ******** 6 A.BOIS
                            *
                            *** 4 A.AFRIC
```

TREE 4: L=183 CI=.607

```
* 1 OUTGROUP
*                                                         H.S.
*                                              *******************2
*                                      ********9
*                                 ****11       ******** 8 H.ER
*                                 *    *** 7 H.HAB
*                            ****12
*                            *    *
*                        ***13    ******** 5 A.ROB
*                        *   *
************************14   **** 4 A.AFRIC
                         *
                         *   ***************** 3 A.AFAR
                         ***10
                             ******** 6 A.BOIS
```

SECTION 3: VARIABLE TRAITS
ii. ALL TREES OF 184 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 5: L=184 CI=.603

```
* 1 OUTGROUP
*                                                          H.S.
*                                              ******************2
*                                    **********9
*                               ****12         ******* 8 H.ER
*                               *    *
*                           ***13    *** 7 H.HAB
*                           *   *
*                           *   ********* 4 A.AFRIC
***************************14
                            *       ************** 3 A.AFAR
                            *     *10
                            *****11 ************ 6 A.BOIS
                                  *
                                  **** 5 A.ROB
```

TREE 6: L=180 CI=.617

```
* 1 OUTGROUP
*                                                           H.S.
*                                              ******************2
*                                     *********9
*                             *******12        ******** 8 H.ER
*                             *       *
*                         ***13       ** 7 H.HAB
*                         *   *
*                         *   ****** 4 A.AFRIC
*************************14
                          *          ************ 3 A.AFAR
                          *    *****10
                          ****11     ****** 5 A.ROB
                               *
                               ******* 6 A.BOIS
```

```
SECTION 3: VARIABLE TRAITS
ii. ALL TREES OF 184 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 7: L=184 CI=.603


* 1 OUTGROUP
*                                                          H.S.
*                                              ******************2
*                                    **********9
*                              *****12         ******* 8 H.ER
*                              *     *
*                          ***13     *** 7 H.HAB
*                          *   *
**************************14   ******* 4 A.AFRIC
                           *
                           *      ************ 3 A.AFAR
                           ******11
                                  *  ****** 5 A.ROB
                                  **10
                                     *********** 6 A.BOIS


TREE 8: L=183 CI=.607


* 1 OUTGROUP
*                                                       H.S.
*                                             *******************2
*                                   **********9
*                             *****13         ******** 8 H.ER
*                             *     *
*                             *     ** 7 H.HAB
*                             *
*****************************14                    *************3
                              *             ******10      A.AFAR
                              *   *********11      ****** 5
                              *   *         *            A.ROB
                              ***12         ****** 6 A.BOIS
                                  *
                                  ***** 4 A.AFRIC
```

SECTION 3: VARIABLE TRAITS
ii. ALL TREES OF 184 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 9: L=184 CI=.603

```
* 1 OUTGROUP
*
*                                 ****************** 2 H.S.
*                           ******9
*                           *     ******** 8 H.ER
*                           *                              A.AFAR
*                           *                        ************3
***************************14                  *****10
                            *         ********11     ****** 5
                            *         *        *         A.ROB
                            *  ******12        ****** 6 A.BOIS
                            *  *      *
                            **13      ***** 4 A.AFRIC
                               *
                               *** 7 H.HAB
```

TREE 10: L=184 CI=.603

```
* 1 OUTGROUP
*
*                      ********** 2 H.S.
*                      *                                  A.AFAR
*                      *                             ************3
*                      *                            *9
*                      *                   ********10**********6
**********************14                   *        *     A.BOIS
                       *               ***11        *** 5 A.ROB
                       *               *   *
                       *       *******12   ****** 4 A.AFRIC
                       *       *       *
                       *******13       *** 7 H.HAB
                               *
                               ***** 8 H.ER
```

SECTION 3: VARIABLE TRAITS
ii. ALL TREES OF 184 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 11: L=182 CI=.610

```
* 1 OUTGROUP
*
*                     ********* 2 H.S.
*                     *                                    A.AFAR
*                     *                                **********3
*                     *                           *****9
*                     *                   *******10    ***** 5
*********************14                   *       *       A.ROB
                      *              ****11       ***** 6 A.BOIS
                      *              *    *
                      *       ******12    ***** 4 A.AFRIC
                      *       *      *
                      *******13      **** 7 H.HAB
                              *
                              ***** 8 H.ER
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY (see page 319)

i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)

TREE 1: L=365 CI=.608

```
* 1 OUTGROUP
*                                                          H.S.
*                                               *****************2
*                                        *******9
*                                 ******10      ******* 8 H.ER
*                                 *      *
*                         *******11      **** 7 H.HAB
*                         *       *
*                     ***12       ****** 4 A.AFRIC
*                     *   *
*                ****13   ******** 6 A.BOIS
*                *    *
****************14    ********* 3 A.AFAR
                 *
                 ******** 5 A.ROB
```

TREE 2: L=365 CI=.608

```
* 1 OUTGROUP
*                                                          H.S.
*                                            ********************2
*                                     *******9
*                              ******11      ********* 8 H.ER
*                              *      *
*                       ******12      ***** 7 H.HAB
*                       *      *
*                   ***13      ******** 4 A.AFRIC
*                   *   *
*                   *   *    ************ 5 A.ROB
*******************14   ****10
                    *        ******* 6 A.BOIS
                    *
                    ************ 3 A.AFAR
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 3: L=359 CI=.618

```
* 1 OUTGROUP
*                                                          H.S.
*                                            ********************2
*                                   *********9
*                            ******11        ********8 H.ER
*                            *      *
*                      *****12      ****** 7 H.HAB
*                      *     *
*                  ***13     ********* 4 A.AFRIC
*                  *   *
*                  *   *   ************* 3 A.AFAR
******************14   ***10
                   *       *********** 6 A.BOIS
                   *
                   ********** 5 A.ROB
```

TREE 4: L=365 CI=.608

```
* 1 OUTGROUP
*                                                            H.S.
*                                           *********************2
*                                  *********9
*                             ****11        ********* 8 H.ER
*                             *    *
*                         ***12    ****** 7 H.HAB
*                         *   *
*                    ****13   *********** 4 A.AFRIC
*                    *    *
********************14    *********** 5 A.ROB
                     *
                     *    ****************** 3 A.AFAR
                     ****10
                          *********** 6 A.BOIS
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 5: L=365 CI=.608

```
* 1 OUTGROUP
*                                                           H.S.
*                                          **********************2
*                               ***********9
*                           ***11          ******** 8 H.ER
*                           *   *
*                     *****13   ******* 4 A.AFRIC
*                     *     *
*                     *     *     ************* 5 A.ROB
*********************14     *****12
                      *           ***** 7 H.HAB
                      *
                      *    *************** 3 A.AFAR
                      ****10
                           *********** 6 A.BOIS
```

TREE 6: L=365 CI=.608

```
* 1 OUTGROUP
*                                                          H.S.
*                                             *******************2
*                                  ***********9
*                             ****11          ******** 8 H.ER
*                             *    *
*                       *****12    *** 7 H.HAB
*                       *     *
*                  ****13     ******** 5 A.ROB
*                  *    *
*                  *    *     ************** 3 A.AFAR
******************14    *****10
                   *          ********* 6 A.BOIS
                   *
                   ******* 4 A.AFRIC
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 7: L=361 CI=.615

```
* 1 OUTGROUP
*                                                          H.S.
*                                          **********************2
*                                  ********9
*                                  *       ********* 8 H.ER
*                          *******12
*                          *       *   ************** 5 A.ROB
*                    *****13       ***11
*                    *     *           *** H.HAB
*                    *     *
********************14     ******* 4 A.AFRIC
                     *
                     *    ************** 3 A.AFAR
                     ****10
                          ************* 6 A.BOIS
```

TREE 8: L=362 CI=.613

```
* 1 OUTGROUP
*                                                           H.S.
*                                            ********************2
*                                 ***********9
*                              **11          ********* 8 H.ER
*                              *  *
*                      *******12  ** 7 H.HAB
*                      *       *
*                 ****13       *********** 5 A.ROB
*                 *    *
*****************14    ******* 4 A.AFRIC
                  *
                  *    ************* 3 A.AFAR
                  ****10
                       *********** 6 A.BOIS
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 9: L=363 CI=.612

```
* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                               ************9
*                         *****12           ********** 8 H.ER
*                         *     *
*                   *****13     ** 7 H.HAB
*                   *     *
*                   *     ********** 5 A.ROB
*******************14
                    *            ************** 3 A.AFAR
                    *    *******10
                    ****11       ************ 6 A.BOIS
                         *
                         ******** 4 A.AFRIC
```

TREE 10: L=365 CI=.608

```
* 1 OUTGROUP
*                                                           H.S.
*                                          **********************2
*                                ***********9
*                           ****12         ********** 8 H.ER
*                           *    *
*                           *    **** 7 H.HAB
*                     *****13
*                     *     *              *************** 3
*                     *     *         ****10             A.AFAR
*********************14     *********11    ********** 6 A.BOIS
                      *               *
                      *               ******* 5 A.ROB
                      *
                      ******** 4 A.AFRIC
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 11: L=362 CI=.613

```
* 1 OUTGROUP
*                                                           H.S.
*                                          **********************2
*                                 *********9
*                          ******12        ********* 8 H.ER
*                          *      *
*                    *****13      ****** 7 H.HAB
*                    *     *
*                    *     ********** 4 A.AFRIC
********************14
                     *          **************** 3 A.AFAR
                     *      ***10
                     ******11   ********** 6 A.BOIS
                            *
                            ********* 5 A.ROB
```

TREE 12: L=365 CI=.608

```
* 1 OUTGROUP
*                                                          H.S.
*                                          **********************2
*                                  ********9
*                           ******11       ********* 8 H.ER
*                           *      *
*                     *****13      ********* 4 A.AFRIC
*                     *     *
*                     *     ***** 7 H.HAB
*********************14
                      *          **************** 3 A.AFAR
                      *     ****10
                      *****12    ********** 6 A.BOIS
                            *
                            ******* 5 A.ROB
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
i. ALL TREES REQUIRING 365 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 13: L=361 CI=.615

```
* 1 OUTGROUP
*                                                          H.S.
*                                          **********************2
*                                  ********9
*                          *******12       ********* 8 H.ER
*                          *       *
*                    *****13       ***** 7 H.HAB
*                    *     *
********************14     ******** 4 A.AFRIC
                     *
                     *     *********** 3 A.AFAR
                     *****11
                           *       ************* 5 A.ROB
                           *******10
                                   ******* 6 A.BOIS
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY

ii. ALL TREES OF 374 STEPS OR LESS (NEW ANCESTOR)(see page 326)

TREE 1: L=368 CI=.620

```
* 1 OUTGROUP
*                                                            H.S.
*                                            ********************2
*                                     *******9
*                              ******11      ********* 8 H.ER
*                              *      *
*                        *****12      ***** 7 H.HAB
*                        *     *
*                    ***13     ******** 4 A.AFRIC
*                    *   *
*                    *   *   ************ 3 A.AFAR
********************14   ***10
                     *       ********** 6 A.BOIS
                     *
                     ********* 5 A.ROB
```

TREE 2: L=374 CI=.610

```
* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                                ***********9
*                             **11          ******** 8 H.ER
*                             *  *
*                       *****13  ******** 4 A.AFRIC
*                       *     *
*                       *     *    ************ 5 A.ROB
***********************14     ****12
                        *          ***** 7 H.HAB
                        *
                        *    ************** 3 A.AFAR
                        ****10
                             *********** 6 A.BOIS
```

```
SECTION 4A: ALL TRAITS: CODED SEPARATELY
ii. ALL TREES OF 374 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 3: L=374 CI=.610


* 1 OUTGROUP
*                                                         H.S.
*                                              ******************2
*                                    **********9
*                              *****11          ******* 8 H.ER
*                              *     *
*                         ****12     ** 7 H.HAB
*                         *    *
*                    ****13    ******** 5 A.ROB
*                    *    *
*                    *    *    **************3 A.AFAR
********************14    ****10
                     *         ********* 6 A.BOIS
                     *
                     ******* 4 A.AFRIC


TREE 4: L=370 CI=.616


* 1 OUTGROUP
*                                                            H.S.
*                                           *********************2
*                                   ********9
*                                   *       ********* 8 H.ER
*                           *******12
*                           *       *   ************** 5 A.ROB
*                      ****13       ***11
*                      *    *           *** 7 H.HAB
*                      *    *
**********************14    ******** 4 A.AFRIC
                       *
                       *   ************* 3 A.AFAR
                       ***10
                           ************ 6 A.BOIS
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
ii. ALL TREES OF 374 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 5: L=371 CI=.615

```
* 1 OUTGROUP
*                                                           H.S.
*                                             *******************2
*                                  ***********9
*                               **11          ******** 8 H.ER
*                               *  *
*                        ******12  ** 7 H.HAB
*                        *      *
*                   ****13      *********** 5 A.ROB
*                   *    *
*******************14    ******* 4 A.AFRIC
                    *
                    *    ************ 3 A.AFAR
                    ****10
                         ********** 6 A.BOIS
```

TREE 6: L=372 CI=.613

```
* 1 OUTGROUP
*                                                           H.S.
*                                            ********************2
*                                ************9
*                           ****12           ******** 8 H.ER
*                           *    *
*                     *****13    *** 7 H.HAB
*                     *     *
*                     *     ********** 5 A.ROB
*********************14
                      *           ************** 3 A.AFAR
                      *    ******10
                      ****11      ************ 6 A.BOIS
                           *
                           ******* 4 A.AFRIC
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
ii. ALL TREES OF 374 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 7: L=374 CI=.610

```
* 1 OUTGROUP
*                                                            H.S.
*                                          *********************2
*                                **********9
*                            ***12         ********* 8 H.ER
*                            *   *
*                            *   **** 7 H.HAB
*                      *****13
*                      *     *             *************** 3
*                      *     *        ****10            A.AFAR
***********************14     ********11    ********* 6 A.BOIS
                        *              *
                        *              ******** 5 A.ROB
                        *
                        ******* 4 A.AFRIC
```

TREE 8: L=372 CI=.613

```
* 1 OUTGROUP
*                                                           H.S.
*                                          *********************2
*                                  ********9
*                           ******12       ********* 8 H.ER
*                           *      *
*                      ****13      ***** 7 H.HAB
*                      *    *
*                      *    ********** 4 A.AFRIC
***********************14
                        *         *************** 3 A.AFAR
                        *     ***10
                        *****11   ********** 6 A.BOIS
                              *
                              ********* 5 A.ROB
```

SECTION 4A: ALL TRAITS: CODED SEPARATELY
ii. ALL TREES OF 374 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

TREE 9: L=371 CI=.615

```
* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                                   ********9
*                            ******12       ********* 8 H.ER
*                            *      *
*                       ****13      ***** 7 H.HAB
*                       *    *
***********************14    ******* 4 A.AFRIC
                        *
                        *     ********** 3 A.AFAR
                        *****11
                              *      ************* 5 A.ROB
                              ******10
                                     ****** 6 A.BOIS
```

SECTION 4B: ALL TRAITS: SAME CODE (see page 326)

i. ALL TREES REQUIRING 318 OR FEWER STEPS (COMBINED ANCESTOR)

TREE 1: L=318 CI=.629

```
* 1 OUTGROUP
*                                                          H.S.
*                                               *****************2
*                                      *********9
*                                *****10         ****** 8 H.ER
*                                *     *
*                         ******11     **** 7 H.HAB
*                         *      *
*                     ***12      ***** 4 A.AFRIC
*                     *   *
*                 ***13   ******* 6 A.BOIS
*                 *   *
*****************14   *********** 3 A.AFAR
                  *
                  ******* 5 A.ROB
```

TREE 2: L=318 CI=.629

```
* 1 OUTGROUP
*                                                            H.S.
*                                               *****************2
*                                      *********9
*                                 ****10         ****** 8 H.ER
*                                 *    *
*                           *****11    **** 7 H.HAB
*                           *     *
*                      ****12     ****** 4 A.AFRIC
*                      *    *
*                 ****13    *********** 3 A.AFAR
*                 *    *
*****************14    ******* 6 A.BOIS
                  *
                  ******* 5 A.ROB
```

SECTION 4B: ALL TRAITS: SAME CODE
i. ALL TREES REQUIRING 318 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 3: L=315 CI=.635

```
* 1 OUTGROUP
*                                                            H.S.
*                                            ********************2
*                                   *********9
*                             *****11        ******** 8 H.ER
*                             *     *
*                      ******12     **** 7 H.HAB
*                      *      *
*                  ***13      ******* 4 A.AFRIC
*                  *   *
*                  *   *  ************** 3 A.AFAR
******************14   **10
                   *      ********** 6 A.BOIS
                   *
                   ********* 5 A.ROB
```

TREE 4: L=316 CI=.633

```
* 1 OUTGROUP
*                                                            H.S.
*                                           *********************2
*                                 **********9
*                                 *         ******** 8 H.ER
*                          ******12
*                          *      *  ************ 5 A.ROB
*                     ****13      **11
*                     *    *         **** 7 H.HAB
*                     *    *
*********************14    ****** 4 A.AFRIC
                      *
                      *   *************** 3 A.AFAR
                      ***10
                          ********** 6 A.BOIS
```

```
SECTION 4B: ALL TRAITS: SAME CODE
i. ALL TREES REQUIRING 318 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED


TREE 5: L=317 CI=.631


* 1 OUTGROUP
*                                                            H.S.
*                                            ********************2
*                                 ***********9
*                              **11          ******** 8 H.ER
*                              *  *
*                       ******12  ** 7 H.HAB
*                       *      *
*                   ***13      ********** 5 A.ROB
*                   *   *
*******************14   ****** 4 A.AFRIC
                    *
                    *   *************** 3 A.AFAR
                    ***10
                        ********* 6 A.BOIS


TREE 6: L=318 CI=.629


* 1 OUTGROUP
*                                                            H.S.
*                                           *********************2
*                               ************9
*                          ****12           ******** 8 H.ER
*                          *    *
*                     ****13    *** 7 H.HAB
*                     *    *
*                     *    ********** 5 A.ROB
*********************14
                      *         **************** 3 A.AFAR
                      *   *****10
                      ***11     *********** 6 A.BOIS
                          *
                          ****** 4 A.AFRIC
```

```
SECTION 4B: ALL TRAITS: SAME CODE
i. ALL TREES REQUIRING 318 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED


TREE 7: L=316 CI=.633


* 1 OUTGROUP
*                                                           H.S.
*                                          **********************2
*                                **********9
*                          *****12         ******** 8 H.ER
*                          *     *
*                    *****13     ***** 7 H.HAB
*                    *     *
*                    *     ********* 4 A.AFRIC
********************14
                     *        **************** 3 A.AFAR
                     *     **10
                     *****11  ********** 6 A.BOIS
                           *
                           ******** 5 A.ROB


TREE 8: L=318 CI=.629


* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                                  *********9
*                          *******12        ******** 8 H.ER
*                          *       *
*                    *****13       **** 7 H.HAB
*                    *     *
*                    *     ****** 4 A.AFRIC
********************14
                     *          ************* 3 A.AFAR
                     *    *****10
                     ****11     ********** 5 A.ROB
                          *
                          ******** 6 A.BOIS
```

SECTION 4B: ALL TRAITS: SAME CODE
i. ALL TREES REQUIRING 318 OR FEWER STEPS (COMBINED ANCESTOR)
CONTINUED

TREE 9: L=318 CI=.629

```
* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                                 **********9
*                          ******12         ******** 8 H.ER
*                          *      *
*                     ****13      ***** 7 H.HAB
*                     *    *
*********************14    ******** 4 A.AFRIC
                      *
                      *    ************* 3 A.AFAR
                      ****11
                           *     *********** 5 A.ROB
                           *****10
                                 ******* 6 A.BOIS
```

SECTION 4B: ALL TRAITS: SAME CODE

ii. ALL TREES OF 323 STEPS OR LESS (NEW ANCESTOR) (see page 329)

TREE 1: L=323 CI=.628

```
* 1 OUTGROUP
*                                                            H.S.
*                                               *****************2
*                                       ********9
*                                 *****10       ****** 8 H.ER
*                                 *     *
*                          ******11     **** 7 H.HAB
*                          *      *
*                       **12      ***** 4 A.AFRIC
*                       *  *
*                  ****13  ******* 6 A.BOIS
*                  *    *
******************14    ********** 3 A.AFAR
                   *
                   ****** 5 A.ROB
```

TREE 2: L=322 CI=.630

```
* 1 OUTGROUP
*                                                           H.S.
*                                               *****************2
*                                       ********9
*                                 *****10       ****** 8 H.ER
*                                 *     *
*                            ****11     **** 7 H.HAB
*                            *    *
*                      *****12    ******* 4 A.AFRIC
*                      *     *
*                  ***13     ********** 3 A.AFAR
*                  *   *
******************14   ******* 6 A.BOIS
                   *
                   ******* 5 A.ROB
```

SECTION 4B: ALL TRAITS: SAME CODE
ii. ALL TREES OF 323 STEPS OR LESS (NEW ANCESTOR)
CONTINUED

```
TREE 3: L=319 CI=.636


* 1 OUTGROUP
*                                                            H.S.
*                                             *******************2
*                                    *********9
*                             ******11        ******* 8 H.ER
*                             *      *
*                       *****12      **** 7 H.HAB
*                       *     *
*                   ***13     ******* 4 A.AFRIC
*                   *   *
*                   *   * ************** 3 A.AFAR
*******************14   *10
                    *     ********** 6 A.BOIS
                    *
                    ******** 5 A.ROB


TREE 4: L=320 CI=.634


* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                                  *********9
*                                  *        ******** 8 H.ER
*                           ******12
*                           *      *  ************ 5 A.ROB
*                      ****13      **11
*                      *    *         *** 7 H.HAB
*                      *    *
**********************14    ****** 4 A.AFRIC
                       *
                       *   *************** 3 A.AFAR
                       ***10
                           ********** 6 A.BOIS
```

```
SECTION 4B: ALL TRAITS: SAME CODE
ii. ALL TREES OF 323 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 5: L=321 CI=.632


* 1 OUTGROUP
*                                                           H.S.
*                                             *******************2
*                                  ***********9
*                               **11          ******* 8 H.ER
*                               *  *
*                        ******12  ** 7 H.HAB
*                        *      *
*                    ***13      ********** 5 A.ROB
*                    *   *
********************14   ****** 4 A.AFRIC
                     *
                     *  *************** 3 A.AFAR
                     **10
                        ********* 6 A.BOIS


TREE 6: L=322 CI=.630


* 1 OUTGROUP
*                                                           H.S.
*                                           *********************2
*                                ***********9
*                           ****12          ******** 8 H.ER
*                           *    *
*                      ****13    ** 7 H.HAB
*                      *    *
*                      *    ********* 5 A.ROB
**********************14
                       *         *************** 3 A.AFAR
                       *  ******10
                       **11      ********** 6 A.BOIS
                          *
                          ******* 4 A.AFRIC
```

```
SECTION 4B: ALL TRAITS: SAME CODE
ii. ALL TREES OF 323 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 7: L=321 CI=.632


* 1 OUTGROUP
*                                                            H.S.
*                                           *********************2
*                                 **********9
*                           *****12         ******** 8 H.ER
*                           *     *
*                     *****13     **** 7 H.HAB
*                     *     *
*                     *     ********* 4 A.AFRIC
*********************14
                      *        **************** 3 A.AFAR
                      *     **10
                      *****11  ********** 6 A.BOIS
                            *
                            ********* A.ROB


TREE 8: L=322 CI=.630


* 1 OUTGROUP
*                                                           H.S.
*                                            ********************2
*                                  **********9
*                           ******12         ******* 8 H.ER
*                           *      *
*                     *****13      ***** 7 H.HAB
*                     *     *
*                     *     ****** 4 A.AFRIC
*********************14
                      *         ************** 3 A.AFAR
                      *    ****10
                      ****11    *********** 3 A.ROB
                           *
                           ******* 6 A.BOIS
```

```
SECTION 4B: ALL TRAITS: SAME CODE
ii. ALL TREES OF 323 STEPS OR LESS (NEW ANCESTOR)
CONTINUED


TREE 9: L=323 CI=.628


* 1 OUTGROUP
*                                                           H.S.
*                                            ********************2
*                                  **********9
*                           ******12         ******* 8 H.ER
*                           *      *
*                       ***13      **** 7 H.HAB
*                       *   *
***********************14   ******** 4 A.AFRIC
                        *
                        *    ************ 3 A.AFAR
                        ****11
                             *    ************ 5 A.ROB
                             ****10
                                  ******* 6 A.BOIS
```