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I am submitting herewith a dissertation written by Steven Mark Donnelly entitled "Size and Shape Variation in Early East African *Homo* and the Validity of *Homo habilis* as a Single Species." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Anthropology.

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We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor
and Dean of the Graduate School

SIZE AND SHAPE VARIATION IN EARLY EAST AFRICAN *HOMO* AND THE VALIDITY OF *HOMO HABILIS* AS A SINGLE SPECIES

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Steven Mark Donnelly

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This dissertation is dedicated to my wife

Sharon Donnelly

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ABSTRACT

The integrity of *Homo habilis* has been the subject of a debate that began more than thirty years ago when the species was first identified and described by Leakey, Tobias and Napier (1964). Within the collection of fossils that have been attributed to *Homo habilis* there is so much variation in size and shape that many paleoanthropologists believe that more than one species is represented. There have been a number of attempts to demonstrate this, but none of these has been able to conclusively demonstrate that the magnitude of variation in *Homo habilis* is *significantly* greater, or that the pattern of variation is *significantly* different from the pattern seen in modern hominoids. Consequently, many paleoanthropologists remain unconvinced, arguing that the variation in *Homo habilis* reflects nothing more than sexual dimorphism, polytypism and evolutionary change within a single lineage.

In this dissertation these competing hypotheses are evaluated by using computer-intensive randomization methods and univariate and multivariate statistics to compare variation in *Homo habilis* with variation in modern hominoids and fossils hominids. Randomization methods and univariate statistics are used to compare the magnitude of variation in the *Homo habilis* dental sample with variation in two extant species of hominoids, *Pan troglodytes* and *Gorilla gorilla,* and one fossil hominid, *Australopithecus robustus*. Multivariate statistics and randomization methods are used to compare the size and shape differences between KNM-ER 1470, the largest cranium attributed to *Homo habilis*, and three smaller crania, KNM-ER 1805, KNM-ER 1813 and OH 24, with size and shape differences between individuals in samples of modern hominoids. For the face and vault the multivariate distances between the fossils are partitioned into 'size' and 'shape' distances whose significance is determined by comparing them with distributions of size and shape distances between individuals in reference samples representing modern *Homo*, *Pan*, *Pongo*

and *Gorilla*. The multivariate distances between the *Homo habilis* crania are also compared with multivariate distances between other Plio-Pleistocene hominids.

The results of the univariate and multivariate comparisons strongly suggest that there is more variation in the *Homo habilis* cranial and dental sample than is reasonable for a single hominoid species. The dental comparisons show that the degree of relative variation in the buccolingual diameter of P_4 is significantly greater than it is in any of the reference groups, even the strongly dimorphic gorillas. The pattern of variation in the early *Homo* dental sample also appears to be unlike the pattern seen in the reference samples, and this also suggests that more than one species is represented.

The results of the multivariate comparisons with the modern hominoids provide the strongest evidence for multiple species of early *Homo*. These comparisons demonstrate that in both the vault and face the size differences, and in some cases the shape differences, between KNM-ER 1470, and the smaller individuals, KNM-ER 1805, 1813 and OH 24, are large when compared to the size and shape differences seen in the extant hominoids, and it is unlikely that KNM-ER 1470 and the smaller specimens could all represent the same species, even if that species were as sexually dimorphic as *Gorilla*.

The size differences between KNM-ER 1470 and the smaller crania are also large when compared to the size differences between fossil hominids that are conspecific, and they are often large when compared to the size differences between fossil hominids that represent different species. The multivariate comparisons of the differences between KNM-ER 1470 and KNM-ER 1805, 1813 and OH 24 with the differences between individuals in the modern hominoids and the fossil hominids demonstrate that it is extremely unlikely that all of these specimens could belong to the same species. Thus, there were at least two lineages of gracile hominids in East Africa during the late Pliocene and early Pleistocene.

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CHAPTER 1

INTRODUCTION

In 1964 Louis Leakey, Phillip Tobias and John Napier identified a new species of hominid, which they named '*Homo habilis*'. This new species was represented by a small collection of fossils from Olduvai Gorge which consisted of three very fragmentary and incomplete crania, two partial mandibles, an isolated molar and some postcranial elements whose association with the cranial remains is unclear. Leakey and his colleagues believed that *Homo habilis* was the earliest and most primitive species of the genus *Homo*, a transitional form which fills the morphological gap between *Australopithecus* and *Homo erectus*. *Homo habilis* also quickly became the subject of a heated controversy. Soon after their paper appeared in *Nature* Leakey, Tobias and Napier were strongly criticized by some of the most prominent paleoanthropologists of that era who felt that they had rash lumped together a few australopithecine and *Homo erectus* fossils to create a species that never existed which filled a morphological gap that also never existed. The views of these critics are succinctly summarized in the words of Brace (Brace et al., 1973) who described *Homo habilis* as "an empty taxon" which was "inadequately proposed and should be formally sunk" (p. 66). Sir Wilfrid Le Gros Clark (1964), who felt that the differences between *H. habilis* and *A. africanus* were 'minor', dismissed the whole issue by stating, "'*Homo habilis*' has received a good deal of publicity since his sudden appearance was announced..... one is led to hope that he will disappear as rapidly as he came. He certainly does not appear to merit a prolonged controversy" (p. 49).

Sir Wilfrid did not get his wish. The integrity of the species *Homo habilis* has been the subject of a prolonged controversy that began with its christening and continues to this day. The early critics were eventually silenced by discoveries in the late 1960's and early 1970's of more complete crania at Olduvai Gorge and East Lake Rudolf (Kenya) which are too primitive to be attributed to *Homo erectus* but too advanced to be australopithecines. Just

as Leakey, Tobias and Napier had argued ten years earlier, *Homo erectus* had been preceded by an earlier and more primitive species of *Homo*. The later discoveries from Olduvai and East Turkana proved, to all but its most inveterate opponents, that *Homo habilis* was a legitimate taxon.

These discoveries however did not put an end to the debate over the integrity of *Homo habilis*, they merely changed its focus. Currently there are many paleoanthropologists who steadfastly believe that all of the East African, non-robust, Plio-Pleistocene hominids represent a single species: *Homo habilis* as defined by Leakey, Tobias and Napier. But even as these new fossils were being discovered and described it became apparent that they make up a rather motley group. So much so that many workers feel that more than one species, possibly even more than one genus, must be represented. Those who argue for a single species claim that the variability seen in *Homo habilis* reflects nothing more than sexual dimorphism, polytypism, intrapopulational variation and the effects of time and evolutionary change within a single species. But those who argue for multiple species counter that the magnitude of variation in these fossils is too great and the pattern of variation too different to accommodate all of them within one species. Therefore, there must have been more than one species of gracile hominid in East Africa during the Plio-Pleistocene. It has been proposed by various experts that there are actually two species of early *Homo*, or perhaps three species of early *Homo*, or possibly one species of early *Homo* and one species of gracile australopithecine. One of these species would be *Homo habilis*, the identity of the other(s) is, like nearly everything else concerning *Homo habilis*, a matter of debate.

There have been a number of attempts to prove that there is more than one species of early *Homo* (Groves, 1989; Groves and Mazák, 1975; Kramer et al., 1995; Lieberman et al., 1988; Rightmire, 1993; Stringer, 1986; Wood, 1985, 1991, 1993). However, none of these studies has provided unequivocal proof that *Homo habilis*, broadly defined, must

represent multiple species because each of them suffers from one (or both) of two shortcomings. First of all there is a disturbing lack of agreement concerning which individual fossils belong to which particular taxon. This confusion is due in large part to the fact that the fossils originally referred to *Homo habilis* by Leakey et al., including the type specimen, are so fragmentary and incomplete. The second problem, which is much more serious, is that none of these studies has been able to conclusively demonstrate that the degree of variation in *Homo habilis* is *significantly* greater than the degree of variation seen in extant species of hominoids, or that the pattern of variation in *Homo habilis* is *significantly* different from the pattern seen in modern hominoids. Each of these studies has its methodological weaknesses, leaving open the possibility that there is only one species of early *Homo* and what seems to be excessive variation in this species may reflect nothing more than random chance in the form of sampling error.

The number of fossils that have been attributed to *Homo habilis* is small. There are for example 15 crania that have been referred to the species but most of these are extremely fragmentary and incomplete; only three of them are relatively intact and one of these is somewhat distorted. Even the dental samples are small. The largest samples are for the molars, for which n is between 7 and 17. Given these small sample sizes it is not surprising that it has proved so difficult to find conclusive quantitative evidence for the existence of multiple species. Most of the studies cited above have either not taken a statistical approach to the problem or have used statistical methods that are inappropriate. Consequently the evidence for multiple species is either difficult to evaluate or inconclusive.

The immediate purpose of the work presented here is to attempt a resolution of the '*Homo habilis* problem'. In large part it represents an extension and elaboration of the work of Kramer, Donnelly, Kidder, Ousley and Olah (1995). In that study we took a novel approach to the problem, using randomization methods to assess the significance of craniometric variation in *Homo habilis*. Unfortunately, as discussed in Chapter 4, the results were

somewhat ambiguous. In this dissertation randomization methods are used to compare dental and craniometric variation in *Homo habilis* with variation in modern hominoids and fossil hominids to determine the probability that *Homo habilis* represents a single species. Given the nature of the data, randomization methods are particularly suitable for this problem. These methods can be used when samples are small, they require no restrictive assumptions about how the data are distributed and they can be used to directly estimate the probability that *Homo habilis* represents a single species.

In this study randomization methods and a univariate measure of variation (the variance) are used to determine if dental variation in *Homo habilis* is significantly greater than that seen in species of modern hominoids and fossil hominids. For these comparisons the test statistic is a univariate measure of variation, and therefore the randomization tests can only be used to determine if the degree of dental variation in early *Homo*, that is if differences in the *size* of the teeth, is significantly greater than is reasonable for a single hominoid species. Randomization methods are also used to compare the differences between the most complete early *Homo* crania with differences between individuals within species of extant hominoids and fossil hominids to estimate the probability that the *Homo habilis* crania could represent a single species. For these comparisons the test statistic is a multivariate measure of distance, and therefore, unlike the dental comparisons, these tests can be used to determine if the degree of variation (i.e. differences in size) or the pattern of variation (i.e. differences in shape) in early *Homo* are consistent with their belonging to a single species. This is accomplished by partitioning the multivariate distances between the early *Homo* crania into size and shape distances, and comparing these with the equivalent distances found within samples of modern hominoids. It has frequently been argued that the magnitude and the pattern of variation in *Homo habilis* are inconsistent with its being a single species. The work presented here represents the first attempt to rigorously and explicitly test these claims within a probabilistic framework.

If the results suggest that *Homo habilis* represents more than one species, there is an additional problem to be addressed, and that is determining which taxa are represented. It is not the primary purpose of this dissertation to classify individual fossils, nevertheless the possible affinities of these specimens is an intriguing problem. Currently, it is not even certain that all of the fossils attributed to *Homo habilis* belong in the genus *Homo*. As a potential first step toward resolving this question multivariate methods are used to compare the more complete *Homo habilis* crania with other Plio-Pleistocene hominids, in the hopes that these phenetic comparisons may provide some insights on the affinities of the specimens attributed to early *Homo*.

The primary purpose of this dissertation is to test the integrity of *Homo habilis* by using randomization methods to determine if the degree and/or pattern of variation in this taxon are significantly different from the degree or pattern of variation seen in species of modern hominoids and fossil hominids. There is however, a much broader and ambitious purpose to this work. The basic problem addressed here, evaluating the meaning of variability in fossils, is not a problem that is somehow unique only to those who are interested in early *Homo*. The problem of species discrimination and recognition is a persistent and ubiquitous problem for paleoanthropologists. This is evident in the fact that virtually every discovery of an important new fossil or group of fossils is followed by a debate over taxonomy and classification, and whether or not the fossils should be recognized as a new species or attributed to a previously recognized taxon. It is also evident in the fact that anytime there is more than trivial variation in a group of fossils there are questions about how many species are represented. The broader purpose of this dissertation is to develop statistical methods that can be used to address questions of taxonomic heterogeneity in the kinds of fossil samples that paleoanthropologists must work with. These methods, as discussed in Chapter 2, have their own limitations, but they do offer a relatively rigorous means of

determining if variation in a group of fossils, or if the differences between two individual fossils, can reasonably be viewed as evidence of multiple species. Potentially, these methods could be used to address many of the current questions in paleoanthropology.

CHAPTER 2

SPECIES, SPECIES CONCEPTS AND SPECIES RECOGNITION

> *The species concept is focal in evolutionary studies and, indeed, in all biological thought. Its endless discussion is sometimes boring and seemingly fruitless, but it is not wholly futile.* (Simpson, 1951, p. 285)
>
> *(I)n no other science has there been as much empty verbiage about the meaning of a word as there has been in taxonomy about the meaning of 'species'.* (Hull, 1965, p. 314)

The problem of the nature and definition of the species has been the center of more attention, debate and dissension, and has probably consumed more paper than any other topic in biology. The purpose of this chapter is not to give a comprehensive, or even extensive review of the 'species problem'. It is merely to touch on those issues that are relevant to the problem of species recognition in paleoanthropology. This is necessary for two reasons. First of all, it is important to be very clear about the species concept that is being used here and the rationale for choosing this concept over other possible species definitions that may also be applicable. The statement (for example) that "KNM-ER 1470 and KNM-ER 1813 are unlikely to be members of the same species" will mean different things depending on how the term 'species' is defined. It could mean that they are reproductively isolated from one another, or that they inhabit different ecological niches, or that they have different mate recognition systems, or that they are 'diagnosably different', or that they are members of separate and independent evolutionary lineages. The species definition used here is an evolutionary species concept similar to the definition proposed by Simpson (1951): A species is an historical entity, an ancestral-descendant sequence of populations (a lineage) which is independent of other such lineages and which has its own evolutionary tendencies and fate. Therefore, the hypothetical statement about KNM-ER 1470 and KNM-ER 1813 would simply mean that they belong to separate, independent evolutionary lineages. These lineages may or may not be capable of interbreeding, inhabit

different ecological niches, have different mate recognition systems or be diagnosably different.

A discussion of the species problem is also necessary in order to provide a justification for the methods used here as tests for multiple species of early *Homo*. Obviously, the species concept should be consistent with the criteria used to recognize multiple species. As discussed below however, there is often a complicated and sometimes rather insidious relationship between how one views the evolutionary process, the species concepts one employs, and the criteria by which species are recognized or delimited. Failure to be aware of these relationships can lead to confusion or even a subtle kind of nonsense, particularly when one is vague about the species concept being used, or switches from one concept to another.

What *is* a Species?

The species category and species taxa

There is more than one meaning to the word *species* as it is used in evolutionary biology and taxonomy. The species is one of the levels or categories of the classificatory hierarchy. Species are also the objects which are classified. The distinction can be made clear by referring to the former as the species category, and the latter as species taxa (Mayr, 1963). The species category is a class, membership in which depends upon a taxon meeting specific criteria. These criteria allow us to identify particular taxa as belonging to the species category rather than some other taxonomic category, such as the genus or family. The species category can be defined, but there is a great deal of disagreement about *how* it should be defined. This is the central issue around which the 'species problem' revolves.

A species taxon is an example or instance, one of many possible members of the species category. *Homo sapiens* is one example of the species category; *Canis familiaris* is another. Species taxa cannot be defined by the physical characteristics of its members, they can only be identified by them (Hull, 1975, 1978; Ghiselin, 1984). A particular species

taxon is identified as an example of the species category because the individual organisms that belong to it share certain traits, but these traits do not define the species, they merely describe and identify it. When a species is given a name a description and diagnosis are also usually given. The description is a lengthy characterization of a taxon, including reference to characteristics which are easily recognizable and comparable, to known variability within populations and between populations, to various morphs, and to traits which can help in distinguishing sibling species. The diagnosis is a much shorter and selective list of traits chosen primarily to help differentiate a taxon from its nearest neighbors of the same rank (Hull, 1978; Ghiselin, 1984).

The traits listed in the description and diagnosis are important for several reasons; they identify species, delimit the boundaries between them and make it possible to classify individual organisms. But they do not define the species; they are not essential properties which each and every member of a given species must have in order to be classified as belonging to that species and no other.

> As important as the traits listed in diagnoses and descriptions may be for a variety of purposes, they are not definitions. Organisms could possess these traits and not be included in the taxon; conversely, organisms could lack one or more of these traits and be clear cut instances of the taxon. They are, as the name implies, *descriptions*. As descriptions, they change through time as the entities which they describe change (Hull, 1978, pp. 352-353, emphasis in the original).

The only essential property that an individual organism must have to be classified as a member of a particular species is genealogical. A group of individuals are members of the same species taxon because they are all from the same part of the 'genealogical nexus' (Hull, 1975, 1978); they are part of the same historical entity and are related to one another by descent. That is why they are similar to one another.

Species are identified, described and diagnosed based on their morphology, but the traits that characterize a species taxon do not define it unless one is using a morphological (or essentialistic/ typological) species concept (Mayr, 1963). Although morphological species

concepts do have their advocates (e.g. Sokal and Crovello, 1970) they simply do not represent biological reality very well. If for no other reason these concepts fail because they do not and cannot take into account the fact that there is variation within species, between individuals at any one point in time and space and across space and time as well. Therefore no species can be adequately defined by morphology alone (Sober, 1980). It is true that inferences about the species status of a group or groups of organisms are based on morphology, and the morphological and phenetic differences between populations will usually determine the number of species recognized. This does not mean however, [contra Sokal and Crovello (1970)], that one is using a morphological or phenetic definition of the species category. The basis for the definition of the species category is not equivalent to the evidence used to make decisions as whether a particular group of individuals satisfy that definition (Hull, 1965; Simpson, 1951, 1961; Wiley, 1978). The evidence of species status may be morphological, "but to conclude that one therefore is using or should use a morphological concept of the category (not taxon) species is either a confusion in thought or an unjustified relapse into typology" (Simpson, 1961, pp. 150-151).

This may seem to be a minor point, but it is actually quite important. In paleoanthropology descriptions and diagnoses are sometimes treated as though they are definitions, and authors may describe species as being 'defined' by the possession of particular traits. But this is confusing the causes of interspecific differentiation with its results. Species are morphologically different from one another because they are different species; i.e. they are separate and independent historical entities. They are not different species because they are morphologically different. Failure to appreciate this distinction results in morphological differentiation being equated with speciation and differences between individuals are treated as though they must be interspecific. Consequently, individuals that are different from one another are attributed to different species because they are different, with very little consideration given to the possibility that the differences

might be intraspecific and due to polymorphism, polytypism or evolutionary change through time. As a result, an unrealistic number of species may be identified or 'defined'.

Defining the species category

There are many ways in which the species category has been defined and many species concepts have been proposed. There is the phenetic species concept (Sokal and Crovello, 1970); the biological species concept (Mayr, 1963); the ecological species concept (Van Valen, 1976); the evolutionary species concept (Simpson, 1951; Wiley, 1978); the recognition species concept (Paterson, 1985); the phylogenetic species concept (Cracraft, 1983, 1989; Nelson and Platnick, 1981; Nixon and Wheeler, 1990); and the cohesion species concept (Templeton, 1989). There is also Kitcher's (1984) cynical species definition: "Species are those groups of organisms which are recognized as species by competent taxonomists. Competent taxonomists, of course, are those who can recognize the true species" (p. 308). Each of these species definitions has its own strengths and weaknesses and each has its proponents and critics. There has always been a great deal of disagreement and debate among taxonomists and evolutionary biologist over which is 'best', and even among the proponents of a particular definition there may be arguments over how the species category can best be defined.

It has been suggested that the reason that there is so little agreement among biologists on this issue is because there is no one 'best' species concept (Kitcher, 1984; Mishler and Donoghue, 1982; O'Hare, 1993). Given the complexity and variety of the living world and the wide diversity of problems that are of interest to biologists it is unlikely that any one species definition can satisfy all the needs of all biologists and be applicable to all organisms and the search for such a definition is probably futile. If we accept this proposition then the species problem is not a problem that needs to be solved, but a problem that needs to be 'gotten over' (O'Hare, 1993). This is essentially what Mishler and Donoghue (1982) were proposing when they suggested that biologists should adopt an attitude of 'pluralistic

realism' about species and species definitions. That is, rather than trying to fit one species definition to all organisms and all problems, taxonomists and evolutionary biologists should use the species concept that is most appropriate for the organisms being studied and the problem of interest.

In the discussion that follows only three species concepts, the biological species concept (BSC), the evolutionary species concept (ESC) and the phylogenetic species concept (PSC), are considered. The BSC is briefly discussed first because it is the species definition most commonly used by biologists and as an integral part of the modern synthesis it has had a tremendous impact on the way in which evolutionary biologists view species and speciation. Consequently, the BSC is the standard against which other species concepts are evaluated. The ESC and the PSC are the species concepts which are most appropriate for fossil species because they are the only definitions that explicitly treat species as historical entities. For the kinds of problems that are addressed in this dissertation the ESC is the most appropriate species concept and discussion of this concept is focussed on what kinds of species and speciation mechanisms are possible under the ESC. The PSC also treats species as historical entities and can be applied to fossil species. However, unlike the ESC, the PSC is very closely linked with a particular systematic philosophy, that of phylogenetic systematics and to a large extent the legitimacy of the PSC depends upon the legitimacy of cladistics. Although the PSC may be the most suitable species definition when the problem of interest is a cladistic analysis of extant species, serious weaknesses emerge when it is applied to fossils. These stem from the fact that the use of cladistic methods is based on a number of simplifying assumptions about what species are, or ought to be, and how morphological evolution and speciation occur, and these assumptions in turn prescribe the kinds of species and speciation processes that are 'permissible'.

The biological species concept

The biological species concept is the species definition that is most commonly used by biologists today. According to Mayr (1963) the concept is biological (as opposed to typological or morphological) because it emphasizes that "the underlying concept is based on the biological meaning of species, that is, to serve as a protective device for a well-integrated, co-adapted set of gene complexes" (p. 20). The BSC recognizes the fact that species consist of populations and the fact that these populations together make up a reproductive community, a genetic community and an ecological community. But the factor that is most important is reproduction. According to proponents of the BSC species maintain their genetic and ecological identity because they are reproductively isolated from other such genetic/ecological communities. For this reason species are defined in terms of reproductive isolation. Species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." (Mayr, 1963, p. 19).

The BSC, like every species concept, has its limitations. Because species are defined by isolation speciation is equated with the acquisition of reproductive isolation. That is, under the BSC isolation is regarded as the cause of speciation or as a necessary precursor of speciation; speciation cannot occur without it. However, in the natural world there does not appear to be any consistent relationship between speciation, differentiation and reproductive isolation, and there are numerous examples of speciation occurring in the absence of isolation (Endler, 1989). Reproductive isolation sometimes follows, rather than precedes, speciation and thus isolation is in some cases the result and not the cause of speciation. In other cases reproductive isolation is never established between species or even higher taxa. According to the BSC reproductive isolation, i.e. the lack of gene flow, is the means by which species maintain their independence from other species, whereas gene flow is the cohesive force through which the populations within a species maintain their identity and which prevents them from evolving independently of one another. However, as discussed

below, there is a great deal of evidence that the importance of gene flow as a cohesive mechanism has been greatly overestimated, in much the same way that the importance of reproductive isolation in speciation has been overestimated.

The evolutionary species concept

The BSC is most appropriate for identifying what Simpson (1951) termed 'non-dimensional' species, that is species which are established in one place at one time, but as he pointed out populations "do have extension in time and space and a non-dimensional taxonomy cannot cope with many essentials of life and its evolution" (Simpson, 1951, p. 289). Lacking the dimension of time the BSC "does not apply, even in principle to temporally sequential species" (Simpson, 1961, p. 150). Without a temporal dimension the BSC, although it may be consistent with evolution, is not an evolutionary species concept. Simpson argued that an adequate species definition should treat species as both genetic communities and evolutionary units. Consequently he proposed that the species should be defined as "a phyletic lineage (ancestral-descendant sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies" (1951, p. 289). This is the evolutionary species concept.

With the ESC the criterion of interbreeding is not definitive in itself, but it is still important because it is one source of evidence as to whether or not the evolutionary definition is satisfied. Reproductive isolation is one way in which a species can maintain its independence from other lineages, and interbreeding can keep populations evolving along the same path of unitary evolutionary role and tendencies. The BSC then is a special case of the ESC, and for this reason species defined by the BSC very often correspond to evolutionary species. However, the ESC is broader than the BSC because it omits the criterion of interbreeding. This is important because interbreeding is not the only way that a species can preserve its unity and independence from other lineages (Endler, 1989; Ehrlich and Raven, 1969; Simpson, 1961).

The ESC introduces the element of time into the concept of species and treats species as historical entities. But the temporal element also creates problems for those who are interested in identifying and classifying fossil species. This is the problem of classifying ancestral and descendant stages in an evolving lineage. With the passage of time and the accumulation of evolutionary change within a lineage descendant populations may become very different from their ancestral populations. The questions that result from this are: (1) should a distinction be made between these populations?; and (2) if such a distinction is needed, how do we make it? Where do we place the boundaries?

Simpson (1951) considered two possible answers to the first question. The first potential solution is to "recognize each evolutionary lineage as a unitary species until it divides and then to consider the descendant branches as distinct from each other and from the single ancestral line" (p. 293) Thus, species originate when they split from the ancestral species and they persist as the same species until they go extinct. As a practical objection to this proposal Simpson argued that in a paleontological sequence the pattern of branching and speciation is gradually discovered and can probably never be completely resolved. If evolutionary species were defined as branches then the taxonomy of fossil species would change every time a new branch was discovered.

As a second objection Simpson noted that a great deal of evolutionary change can occur within a lineage without any splitting. He argued that in such cases it is 'not useful taxonomy' to classify that lineage as a single species throughout its history. His underlying rationale seems to be that to not recognize the differentiated ancestral and descendant populations in an unbranched lineage as separate species is to ignore a very important aspect of evolution. So Simpson's answer to the first question is, yes, we should classify the early and later populations as different species if they are different enough from one another. Simpson termed these 'successional species'; they are also referred to as 'paleospecies' (Cain, 1954) or 'chronospecies' (Raup and Stanley, 1978).

The practical justification for recognizing paleospecies is the argument that within a lineage the morphological differences between early and late populations are often so marked that they would be recognized as separate species *if* they were synchronic (Raup and Stanley, 1978). However, *if* they were synchronic they would also be separated by a discontinuity; there would be an identifiable, nonarbitrary boundary between them. But paleospecies are not synchronic, they are related to one another as ancestor and descendant and because evolutionary change occurs gradually (in terms of generations, but not necessarily on the geological time scale) they are linked together by a graded series of intermediate populations. Because the transition from ancestral to descendant species takes place gradually there is no morphological discontinuity marking the boundary between them. It is true that gaps in the fossil record may give the appearance of morphological gaps and can serve as convenient boundaries between paleospecies, but when the fossil record is relatively complete or when the gaps are filled paleontologists must establish species boundaries in some other way.

Any division of a continuous, evolving lineage will be arbitrary to some degree but the successional species themselves need not be. Simpson (1961) suggested that successive species "should be so defined as to make the morphological difference between them at least as great as sequential differences among contemporaneous species of the same group or closely allied groups." (p. 165). Expanding on this idea Hull (1965) proposed that extant species closely related to the fossils of interest can serve as 'yardsticks' for measuring taxonomic space and determining the species status of the fossils. For example, if the species status of the extant taxa is determined by interbreeding then the unit of taxonomic space is:

> the morphological distance usually indicative of interbreeding status among contemporary organisms which usually reproduce by interbreeding. However, interbreeding is not the unit of taxonomic space; interbreeding merely determines the length of the unit of taxonomic space..... the yardstick is morphological distance. Interbreeding determines how long a yard of morphological space is..... The purpose of the yardstick is to delineate

> evolutionary units. The rationale for making the yardstick one length rather than another is that for the group of organisms in question a particular morphological distance is usually indicative of interbreeding status, which is indicative that the group is evolving as a unit and is, hence, rightly called a species. (Hull, 1965, p. 213)

Thus, the boundaries between successional species may be arbitrary, but the species themselves are not because they have prescribed limits. These limits are set by the degree of morphological variation that is consistent with extant species.

Wiley (1978, 1981) has also been a strong advocate of the ESC. He defined an evolutionary species as "a single lineage of ancestral-descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." (Wiley, 1978, p. 18). This definition is only a slight modification of Simpson's, but in the discussion that follows the definition Wiley explores some of its 'logical corollaries' and reaches very different, and far-reaching conclusions about what kinds of species and speciation processes are allowed for by the ESC.

According to Wiley (1978) one logical corollary of the ESC is that:

> No presumed separate, single, evolutionary lineage may be subdivided into a series of ancestral and descendant "species". This corollary is, perhaps, self-evident and would hardly be worth discussing if it were not for the rather common practice among some paleontologists of subdividing a single lineage into a number of "species" (p. 21).

Thus, where Simpson took the position that the ESC allows for the identification of successive species, and that this is even desirable, Wiley argues that the ESC precludes such species:

> The evolutionary species concept is, of course, diametrically opposite to the notion that phyletic evolution can produce new species. In other words, although I do not deny that phyletic evolution proceeds in lineages, I submit that such a process does not produce the wholesale transformation of the demes of one species into another species. (Wiley, 1981, p. 39)

Wiley's opposition to recognizing successive species is based on three lines of argument. The first has to do with the arbitrariness of successive species. According to Wiley any subdivision of a continuous, evolving lineage must be arbitrary and therefore the species

identified in this way and the speciation mechanisms that give rise to them must also be arbitrary.

> In a phyletically evolving lineage..... exactly where to draw the line between two species is entirely a matter of opinion. How many of these species to recognize is also a matter of opinion. Thus the number of speciation events and the timing of these events is not a subject of scientific inquiry but a matter of personal taste. From the standpoint of the logic of science, such a practice is not acceptable. (Wiley, 1981, p. 40)

Wiley's second objection to successional species is based on the philosophical argument that species are individuals, not classes. This possibility was first raised by Ghiselin (1974) who proposed that (in a logical sense) species taxa are not classes or natural kinds, they are individuals in the same way that single organisms are individuals. According to advocates of the species as individuals (s-a-i) thesis species taxa cannot be classes because they are continuous but limited in space and time, and because membership in a class is contingent upon having certain attributes. However, in every species there is variation at any one point in time and species can also change through time. Therefore, membership in a particular species cannot depend on individuals having certain attributes because those attributes may or may not be present in all members of a species at any one point in time and they may also evolve and change over time.

So, argue the supporters of the s-a-i thesis, species taxa cannot be classes, instead they must be individuals. That is, each species is a particular thing which is denoted by its name and not by its physical attributes or essential properties (Ghiselin, 1974, 1984, 1987; Hull, 1975, 1978). Each is an historical entity with its own spatiotemporal boundaries and each is continuous in time because integrity is maintained by internal cohesive mechanisms that are shared by all of the organisms that are a part of that species (Hull, 1975, 1978). If this is true then it does not matter how much change a lineage undergoes, it must always be the same species (Hull, 1975; 1978; Ghiselin, 1987). An individual cannot gradually change into another individual, and, according to the advocates of the s-a-i thesis, one species cannot gradually evolve into another; no matter how much it might change. A parallel is

often drawn with the ontogeny of an individual organism: No one would argue that Charles Darwin at age 5 and Charles Darwin at age 55 were different individuals, even though physically and behaviorally Darwin at age 55 was very different from himself at age 5. The reason that Charles Darwin was the same individual throughout his life is because his continuity in space and time was maintained. In the same way a species, as long as spatiotemporal continuity is preserved, remains the same species. Within a species the amount of evolutionary change that can potentially occur is unlimited, but no matter how much it changes it will always be the same species. Ghiselin (1987) has even gone so far as to claim that if species are not individuals then they cannot evolve because only individuals can change.

Because the ESC treats species as historical, spatial and temporal entities Wiley (1978, 1981) equates evolutionary species with individuals. Therefore, he argues that the ESC does not allow for the recognition of successive species. An evolutionary species has its origins when it arises by cladogenesis and ceases to exist when it goes extinct; it cannot evolve phyletically into another species. As a final argument against phyletic speciation Wiley (1981) asserts that it has never been adequately demonstrated, citing the model of punctuated equilibria (Eldredge and Gould, 1972; Gould and Eldredge, 1977) as support.

Wiley's arguments against phyletic speciation have been adopted and repeated by a number of paleoanthropologists. This may be due in part to the fact that this view agrees so well with the tenets of punctuated equilibria and phylogenetic systematics, both of which have found widespread acceptance in paleoanthropology. Certainly if the arguments against phyletic speciation are valid then Wiley is correct to assert that identifying successive species is an arbitrary practice that can only obscure and confuse our understanding of how evolution and speciation occur. However, careful examination of his arguments shows that none of Wiley's criticisms can be supported.

The s-a-i thesis is a provocative idea which appears, at first glance, to go a long way to resolving 'the species problem'. But examination of the claims made by its proponents show that species taxa do not meet the conditions of individuality. Species may, in some respects, have some of the properties of individuals, and it may be of heuristic value to treat them as such, but they are not individuals. They do not satisfy all of the conditions of individuality and they are defined, even by the advocates of the s-a-i thesis, by essential properties. Species taxa are classes.

One required condition for individuality is spatial and temporal continuity; but to be an individual continuity must be maintained through space and time by internal cohesive mechanisms (Ruse, 1987). That is, the continuity of an individual is maintained because of causal interactions among its parts. It is for this reason that proponents of the s-a-i thesis emphasize interbreeding as a cohesive mechanism. Interbreeding is an internal cohesive mechanism shared by all members of a species and if continuity is maintained by interbreeding then one of the required conditions for individuality is satisfied. Because of the pervasive influence of the BSC many biologists do emphasize interbreeding as the mechanism through which species maintain cohesion and continuity. However, cohesion can be the result of more than just one factor or process and although gene flow *may* be important for maintaining cohesion and identity in some species so may other factors such as similar selection regimes or developmental constraints.

Ehrlich and Raven (1969; see also Lande, 1980) have argued that the influence and importance of gene flow has been greatly overestimated and that for many species it is not the mechanism that preserves and maintains species integrity. The existence of sibling species and the fact that populations that have been isolated for long periods of time often show little differentiation demonstrate that gene flow cannot always be the cause of phenotypic similarity. Conversely, populations freely interbreeding but under different selective regimes can show marked differentiation. Ehrlich and Raven argue that the

primary cohesive and disruptive force in evolution is selection, and it is selection that determines what influence gene flow, or the lack of it, will have. Lande (1980) has also argued for the primacy of selection as a cohesive force:

> Both theoretical and empirical studies have confirmed that gene flow is not a very effective homogenizing agent against spatially varying selection. When there are appreciable differences in selection between local populations separated by distances much larger than the mean individual dispersal distance, gene flow cannot enforce phenotypic uniformity across the species range..... Conversely, many species with disjunct ranges have maintained phenotypic uniformity despite the lack of gene flow..... (Lande, 1980, p. 464).

> Evolutionary stability of the mean phenotype in a population ultimately depends on stabilizing selection on the phenotype. Thus of the major forces conserving phenotypic uniformity in time and space, stabilizing selection is by far the most powerful. (Lande, 1980, pp. 466-467).

Selection is not an internal cohesive force because it acts on the level of the individual, not the species. If the identity of a species is maintained by selection cohesion is simply the result of similar but independent processes acting on individuals; it is not the result of causal interactions between those individuals (Ereshefsky, 1991; Ruse 1987). If the spatiotemporal continuity of a species is preserved by the external force of selection then that species is not an individual.

The s-a-i thesis is also based on the belief that species cannot be classes because they have spatiotemporal limits and cannot be defined in terms of essential properties. However, in discussions of the s-a-i thesis only physical characteristics are considered as potential essential properties. But even as it is argued that species cannot be defined in terms of essential properties (=physical traits) genealogy is treated as an essential property. Species *are* defined by essential properties, but these essential properties are not physical, they are genealogical. A species is defined by its place in the hierarchy of descent. Therefore species taxa are classes, but they are not universal classes; they are classes which are spatiotemporally continuous, but limited in space and time, and whose members are

connected through descent from a common ancestor but are not necessarily connected causally (Mishler and Donoghue, 1982).

Wiley's second criticism of successional species is that the boundaries between such species, and the species delimited by them, are completely arbitrary. For Wiley the only discrete and nonarbitrary species boundary is the boundary that marks the origin of a new species by cladogenesis. As discussed above, it is true that the boundaries between successive species must be arbitrary to some extent, but they are not entirely so, and the species defined by these boundaries are not arbitrary. In any case, the assertion that branching is the only objective way to identify the origination of a species is inconsistent with the gradual nature of evolutionary change. Because evolution is a gradual process there is no easily identified, definite boundary that marks the division of one lineage into two and in the fossil record the boundary that marks the origin of a new clade is no less arbitrary than the boundary that separates two successional species.

It is a very simple matter to locate the boundary that marks the origin of a new clade or species when it is a node on a cladogram. It is much harder to identify that branching 'event' in the fossil record. When the boundaries between clades do appear to be discrete and real it is only because of the incompleteness of the fossil record, for "even at cladogenesis lineages may diverge gradually and continuously, lacking sharp boundaries between species" (Rose and Bown, 1993, p. 305.). If, for example, there existed a perfect and complete fossil record for two closely related species, we would find that as we trace this fossil record back through time the differences between the two species will disappear, perhaps gradually, perhaps rapidly, as we approach the point of divergence until we no longer have two discrete taxa. At what point then do we draw the boundary that marks the origin of a new species? Any boundary would be arbitrary to some degree because speciation is a process, not an event.

Simons and Rasmussen (1995) have encountered this problem as they have recovered and studied the fossil remains of the very earliest anthropoids:

> The assemblage of anthropoidean attributes observed among extant species, including relatively flat-crowned molar relief, large brains and reduced olfaction, did not characterize the earliest representatives of the suborder and did not evolve together as part of a single adaptive shift or evolutionary jump. Rather, anthropoidean characteristics accumulated piecemeal over millions of years. The evolutionary transition between primate suborders could easily have resulted from known microevolutionary processes rather than from a single or even a few dubious macroevolutionary jumps. The very recognition and easy definition of Anthropoidea as a taxon were, in part, consequences of the extinction of the lineages now being discovered in the African Eocene.....
>
> .....because it is clear that all anthropoidean synapomorphies did not evolve simultaneously, systematists will have to be satisfied with arbitrarily picking one or a few traits of shared derivation to define the suborder (pp. 136-137).

The idea that speciation can only occur through cladogenesis would be more defensible if it could be proven that the evolutionary processes that result in evolutionary change within a lineage are different from those that cause or result from cladogenesis. However, unless one accepts the theory of punctuated equilibria, a theory whose validity has yet to be demonstrated, there is no justification for taking such a position. In every lineage the evolutionary processes that produce change are the same and the only difference between anagenesis and cladogenesis is the number of lineages involved. Ignoring this fact will only create more problems and difficulties than it resolves.

> Consider a case in which an original population is split into two populations. Over time, each of the isolated populations evolves anagenetically and gradually, diverging from the parent population. The evolutionary process in each isolated lineage is the same as in the parent population and must be the same whether or not the other lineage existed. At least one (perhaps both) of the daughter lineages must be a new species, but which one? At what point in either of the now separate lineages has a new species evolved, and how are we to recognize this? Is the species boundary discrete and nonarbitrary? If sufficient evolution occurs in one or both lineages to require recognition of a new species, whatever the criteria (reproductive, morphological), is this transition any different from an equal degree of evolution within a single phyletic lineage? If one of the daughter lineages was not preserved in the fossil record (or had not existed at all), should that alter the species status of the other, which underwent the same process and extent of evolutionary change from the parent population in either case? (Rose and Bown, 1993, p. 301).

From a more practical point of view it should be noted that, because of the incompleteness of the fossil record, it is rarely possible to unequivocally document cladogenesis (Levinton, 1988). Consequently, significant morphological change in any sequence of fossils could be the result of evolution within a single lineage, or it could be the result of a cladogenetic event or multiple cladogenetic events in which the parent species did not persist for very long or was not preserved or has not been discovered.

Wiley's third argument for the invalidity of successional species is the claim that phyletic speciation has never been adequately demonstrated. There are in fact many well documented examples of significant evolutionary change occurring within a single lineage (see for example references in Gingerich, 1985; or Levinton, 1988). In many cases the degree of change is great enough to warrant the recognition of successive species.

The species definition used in this dissertation is an evolutionary definition, but it is one that is more consistent with the views of Simpson than those of Wiley, and the possibility of phyletic speciation is explicitly recognized. This is important because it has been proposed that when testing for multiple species in fossil assemblages paleoanthropologists should use fossils from a restricted timespan in order to minimize the effects of variation due to change through time (e.g. Cope and Lacy, 1992; Miller, 1991). It is also often claimed by those who argue for only one species of early *Homo* that variation within *Homo habilis* is due in part to the effects of time (e.g. Johanson et al., 1987; Tobias, 1991; White et al., 1981; Wolpoff, 1994). However, if there is significant temporal change within a fossil assemblage such that the magnitude of variation is excessive relative to extant species, serious consideration should be given to the possibility of recognizing more than one species even if the fossils do represent a single, undivided lineage.

The phylogenetic species concept

The phylogenetic species concept (PSC) is a direct outgrowth of phylogenetic systematics (cladistics). Like the ESC, the PSC explicitly treats species as historical entities, and because of its emphasis on differentiation and diagnosis it can easily be extended to fossils. A number of phylogenetic species definitions have been formulated (Cracraft, 1983; 1989; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Nixon and Wheeler, 1990), but all are very similar to Cracraft's definition (1989, pp. 34-35): "A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent."

The stated purpose of the PSC is to provide a species concept that is consistent with the principles and aims of phylogenetic systematics (Cracraft, 1983, 1989; Nixon and Wheeler, 1990). Consequently the focus is not on the processes that produce taxa but rather the results of these processes: taxa and clades. Although the PSC places a very strong emphasis on character analysis, and in particular the search for diagnostic characters (apomorphies), the interest is not in the characters themselves, but rather on what they are indicative of: taxonomic units and the relationships among them. In phylogenetic systematics there is ostensibly no concern with evolutionary processes or the mechanisms that produce characters or taxa. The concern is only on identifying taxa and determining how they are related to one another. This is essentially a 'taxic' view of evolution (Szalay, 1993) in which species are treated as though they are individuals; species give rise to species, but (beyond the required assumption that differentiation and speciation always occur by cladogenesis) there is no concern with the processes that cause differentiation and speciation. The interest is on the products of evolution and speciation, groups of organisms which are, "taxonomic entities defined in terms of their evolutionary differentiation from other such forms. These entities should be called species" (Cracraft, 1983, pp. 169-170).

Under the PSC any diagnosably distinct cluster of organisms is a species. The PSC does not allow for the recognition of species that consist of multiple differentiated clusters; there are no polytypic phylogenetic species. For the practitioners of phylogenetic systematics this has two favorable consequences. The first consequence is that the units of classification are also the units of evolution. "Given an isolated population that has evolved one or more apomorphous (derived) characters, most biologists would call it a 'unit of evolution,' in that the primary characteristic of evolution, i.e., the origin of a new taxon and the evolutionary modification of primitive characters, is satisfied" (Cracraft, 1983, p. 164). A species that consists of more than one differentiated population is unsuitable for analyzing the pattern and process of taxonomic differentiation because it is not an evolutionary unit, it is a conglomeration of multiple evolutionary units. According to Cracraft (1983, 1989) the second consequence of the PSC is that a species is more likely to be monophyletic if it is the smallest diagnosable cluster of individual organisms than if it consists of multiple diagnosable clusters.

The PSC cannot be used to identify ancestral species because ancestral species, or ancestral taxa, are paraphyletic and so they are 'not real' (Ax, 1987; Nelson, 1989). "Because paraphyletic taxa fail to include some descendants of the specified common ancestor, they can never be phylogenetic taxa" (De Queiroz and Donoghue, 1990b, p. 68). The PSC also does not allow for the recognition of successional species. If a lineage persists through geologic time without any change in its combination of characters it remains the same species (Nixon and Wheeler, 1990) but if an apomorphy appears within a lineage the earlier part of the lineage, which lacks this apomorphy, must be one species and the later segment which possesses it, and which is therefore diagnosably different, must be another. However, because the assumption is that all differentiation occurs by branching the two species will not be recognized as an ancestor and its descendant, but rather as sister species.

The inability to identify ancestral taxa or successional species is only one of several problems that emerge when the PSC and cladistic methods are applied to fossil data. In order to use cladistic methods it is necessary to make a number of assumptions about speciation and the pattern of evolutionary change. In phylogenetic systematics it is assumed that all differentiation (=speciation) occurs by the dichotomous splitting of lineages and it is assumed that all differentiation occurs at the time of speciation. These are not statements or observations about how evolution occurs that can be tested or demonstrated by cladistic methods, they are necessary assumptions that are required by the methods. Unfortunately it often happens that these assumptions come to be treated as though they are demonstrated facts about evolution. This may be of little consequence when the subject of interest is extant taxa and there is no temporal dimension to consider. But when the PSC and cladistic methods are applied to fossils, where there is a time dimension, where differentiation may not involve branching and may occur in a mosaic fashion over significant periods of time and where some species may be ancestral to others, the consequences are far-reaching. When cladistic methods are used to identify or detect species in the fossil record, or to study the relationships among fossil taxa, a particular evolutionary pattern is imposed on the data because of the assumptions implicit in the analysis. The evolutionary pattern derived from a cladistic analysis of fossils is then often treated as though it were evidence that can tell us something about evolutionary processes or patterns.

This might be justified if it could be shown that the assumptions about the pattern and process of evolution implicit in a cladistic analysis are consistent with evolutionary theory. In fact, the majority of cladists claim that phylogenetic systematistics does not require, and should not be committed to, any particular theory or model of evolutionary processes. Among other things, it is claimed that hypotheses about evolutionary relationships are testable, whereas hypotheses about evolutionary processes are not. "Although I am hardly

arguing that a hypothesis of evolutionary process cannot be formulated within the hypethetico-deductive system, I have not seen such a formulation, and until such a formulation is developed, I will continue to prefer hypotheses that do not rely on particular ideas of evolutionary change" (Gaffney, 1979, pp. 87-88). Therefore, it is argued that phylogenetic systematics, if it is to be rigorously scientific, should concentrate on evolutionary hypotheses that can be tested (hypotheses about relationships) and avoid those that are untestable (hypotheses about processes).

In reality though, advocates of phylogenetic systematics often show a clear and strong preference for the theory of punctuated equilibria (e.g. Cracraft, 1979; Eldredge, 1979, 1993; Wiley, 1979, 1981). This is to be expected since the assumptions of cladistics agree so well with the basic tenets of punctuated equilibria: new species always arise by cladogenesis, all significant morphological change occurs rapidly and at the time of splitting, and the brief episodes of sudden change are followed by long periods of stasis (Eldredge and Gould, 1972; Gould and Eldredge, 1977). If evolution is more complicated than this, if new features evolve gradually through time, in a mosaic fashion and not necessarily at the time of divergence, character distributions will be unclear, and phylogenetic analyses of fossil data will be much more ambiguous in terms of what they tell us about evolutionary processes and patterns. Thus, the theory of punctuated equilibria gives legitimacy to the assumptions that are the basis of cladistic analysis. Unfortunately punctuated equilibria is a theory whose validity has yet to be demonstrated. It is largely untestable, it is completely at odds with the current understanding of population genetics and evolutionary biology, and it is often contradicted by the evidence of the fossil record (Charlesworth, Lande and Slatkin, 1982; Gingerich, 1985; Hecht and Hoffman, 1986; Hoffman, 1989; Levinton, 1988; Maynard Smith, 1988; Stebbins and Ayala, 1981).

A second shortcoming of the PSC arises as a consequence of the attempt to make the species both the unit of classification and the unit of evolution, and identifying differentiated

populations as species because these are evolutionary units. With the PSC any diagnosably distinct group of organisms will be identified as a species because differentiation is the criterion by which species are recognized. But morphological differentiation does not require reproductive isolation, and species identified by the PSC are not necessarily reproductively isolated from one another. "(J)ust because the terminal 'species' of a phylogenetic diagram are drawn on separate branches, this does not necessarily imply that there has been absolutely no gene flow between them" (O'Hare, 1993, p. 243). If there is gene flow among phylogenetic species then the relationships among them are reticulate rather than hierarchical and cladistic analyses, in which only hierarchical relationships can be represented, are inappropriate and misleading. Furthermore, since phylogenetic species may not be reproductively isolated from one another differentiation can be lost through gene flow. If gene flow is absent or weak enough, and/or if selective regimes vary spatially populations will differentiate and be recognized as separate phylogenetic species. But this differentiation will often be ephemeral because patterns of migration between populations can change; barriers to gene flow can disappear or levels of gene flow can increase; and patterns of selection can also vary through time (Futuyma, 1987, 1989). As a result, through time the pattern of morphological differences between populations will be altered by gene flow and fluctuating selection and new patterns of geographical and morphological differentiation will appear. Phylogenetic species may be the units of evolution, but they are often transitory. For fossils the pattern of relationships among populations within a lineage will vary over time and these relationships will be both reticulate and hierarchical. Identifying every differentiated group of fossils within a lineage as a species, with all that the term implies, and imposing a hierarchical pattern of relationships on these 'species', will only distort our view of evolutionary history.

There is no necessary reason why species must be the units of evolution. Evolutionary species are not evolutionary units, they are the entities within which evolutionary change

accumulates and becomes permanent as a result of processes operating at lower levels (Futuyma, 1987, 1989; Hull, 1978). Although populations may be the units of evolution they are not identified as species because they have reticulate relationships and are not evolving independently of one another. Thus, within a lineage there may be many evolutionary units at any one time, but for the most part the evolutionary changes that occur within them are transitory and never become established.

Because of the strong connections between the PSC, phylogenetic systematics and the theory of punctuated equilibria the PSC has its limitations when it is used as the basis for identifying and delineating fossil species. The close ties between the PSC, cladistics and punctuated equilibria also make the PSC an inappropriate definition for detecting or recognizing species. This is the third problem with the PSC that arises when it is applied to fossil data. This problem and its implications are discussed below.

Species concepts and speciation processes

In the discussions and arguments over the 'species problem' that have appeared in print it is quite apparent that there is often a strong and fundamental relationship between species concepts and the processes which are believed to give rise to species. Some species concepts depend on particular mechanisms of speciation and oblige us to adopt certain views of speciation. Consequently, they define the taxonomic patterns that can be seen and, thus the processes that are believed to give rise to these patterns (Chandler and Gromko, 1989). For example, the BSC requires reproductive isolation, both as the mechanism responsible for speciation and the mechanism that maintains species boundaries. The PSC, because of its close ties to phylogenetic systematics, requires that all morphological differentiation occur by branching events and as a result the relationships between taxa must always be hierarchical.

Certainly a species concept should not be incompatible with the facts of evolution. Species taxa are entities which change through time and which are related to one another

through a pattern of common ancestry. A species concept that is inconsistent with these facts is of little use. But at some level a species concept also places constraints on our understanding of speciation by "defining the units or species-determining criteria with which our processes must minimally deal" (Chandler and Gromko, 1989, p. 117).

> (T)he concept defines the arena in which our theories of speciation must compete. Because our conceptual view of species also defines the units which we ultimately include in our evolutionary analyses, it will determine the patterns we seek to explain (Cracraft, 1983, 1987). From a given sample of populations, the BSC, phylogenetic species concept, or recognition species concept are all likely to delimit different patterns of species taxa (patterns of reproductive isolation, patterns of characters states, etc.). Indirectly then these concepts will define a particular universe of processes that will explain the pattern. (Chandler and Gromko, 1989, p. 118)

Any species concept will constrain our views of evolutionary patterns and processes to some degree, but how restrictive these constraints may be is variable, and there is disagreement on the question of how restrictive they ought to be. Some biologists (e.g. Cracraft, 1983; De Queiroz and Donoghue, 1990a, 1990b; Wiley, 1978) have taken the position that species concepts should not be independent of theories about speciation processes and it is argued that to be useful a species concept should place limits on what kinds of speciation processes are permissible. On the other hand, there are those (e.g. Chandler and Gromko, 1989; Mishler and Donoghue, 1982; Wheeler and Nixon, 1990) who believe that no species concept should be burdened with a commitment to a specific mode or process of speciation, nor should the validity of a species concept depend on the validity of a particular theory about evolutionary processes, nor should a particular species concept be adopted because it conveniently fit into some more inclusive theory, such as a theory of evolutionary processes. Tightly linking a species concept to a particular theory of processes will only reflect preconceptions as to which aspects of speciation are most important, or which speciation processes are most frequent, or even which are possible.

I maintain that a species concept should not dictate what kinds of evolutionary processes are possible, and that a species concept is more useful if it is kept logically distinct from

particular mechanisms of speciation. This is an additional justification for using the ESC rather than the PSC or some other species concept. The ESC is not closely linked to any particular theory about evolutionary processes or patterns. It is, like the PSC, a definition which focusses on the products of evolution, independent lineages, rather than the processes of evolution. It is only concerned with the manifestation of cohesion through time, not with the evolutionary mechanisms that are responsible for cohesion. It does not matter if the unity of a lineage is maintained by interbreeding, stabilizing selection, developmental constraints or some other mechanism. The criteria that qualify the members of evolving lineages as different species are not a function of the processes that preserve cohesion within those lineages, nor are they a function of the particular mechanisms that cause lineages to diverge.

Species Recognition in Paleoanthropology

Many of the issues that have been discussed in the literature on the 'species problem' seem to be largely academic and of little relevance to those who are interested in the more mundane and pragmatic problems of paleoanthropology. What does it matter, for example, if species are individuals or classes, when we are only interested in the practical problem of determining how many species are represented in a collection of fossils? It does matter however, and it is important because there is a subtle but very complex relationship between the positions we take on these more abstract questions and the ways in which we choose to approach the practical problems. Whether we are aware of it or not, the stances we take on the abstract issues determine to a large degree, which problems we think are important and worth addressing, the methods we use to address those problems and the conclusions that we draw from our results.

This complex relationship is evident in the discussions of species recognition that have appeared in the paleoanthropological literature. In recent years, paleoanthropologists have become concerned with both the practical and the theoretical aspects of species recogni-

tion. This must be due in large part to the simple fact that the size of the hominid fossil record has expanded dramatically in the past 25 years, and consequently paleoanthropologists are confronted more often with the problem of evaluating the significance of variation in collections of fossil hominids. The hominids attributed to early *Homo* are an excellent example of this. In the early to middle 1970's work in East Africa resulted in the discovery of a number of relatively large-brained, gracile Plio-Pleistocene hominid fossils. As the number of fossils attributed to early *Homo* increased, and as more complete specimens were recovered, it became evident that within this sample there is a great deal of variation. Just what exactly this variation is indicative of is an issue that remains to be resolved. The interest in the problem of species discrimination may be primarily due to the expansion of the hominid fossil record, but it is also due in part to the growing influence of phylogenetic systematics and the consequent emphasis on reconstructing the pattern of hominid evolution.

When faced with the problem of evaluating the significance of variation in fossil collections there are currently two very different strategies available to paleoanthropologists. The first is based on the use of quantitative measures of variation, such as the coefficient of variation, to determine if variation in the fossils is excessive when compared to variation in extant species that are closely related to the fossils. For hominids, the most appropriate reference species are modern humans and the other large-bodies hominoids. These reference samples provide a baseline against which variation in the fossil samples can be compared. It is usually inferred that the fossils sample more than one species if variation in the fossils appears to be excessive relative to variation in the reference species. The second strategy is a qualitative approach that involves the search for diagnosable clusters of fossils which correspond to phylogenetic species. This method is explicitly based on the PSC and cladistic methods.

Qualitative approaches to species discrimination

More than any other species concept the PSC, by defining species as 'irreducible diagnosable units', provides a very clear and straightforward protocol for recognizing species in the fossil record. The detection and diagnosis of fossil species becomes a simple exercise in character analysis using the principles of cladistics. It is not surprising then that a number of paleoanthropologists, most notably Kimbel (1991; also Kimbel and Rak, 1993) and Tattersall (1986, 1991, 1992), have become strong advocates of the PSC. Those paleoanthropologists who are attracted to the PSC are primarily interested in reconstructing the pattern of hominid evolution through the use of cladistic methods. It is claimed that logically hypotheses about evolutionary patterns must precede those about evolutionary processes. It is argued that the first task of the paleoanthropologist should be to discover the pattern of evolutionary differentiation in the hominid fossil record and only after this is accomplished can we go on to test hypotheses about rates or processes. If the primary focus is on reconstructing the pattern of differentiation, it seems only logical to adopt a species concept which defines species as differentiated units. When defined in this way species are both taxonomic units and evolutionary (phylogenetic) units (Kimbel, 1991).

For those who are interested in recovering the pattern of human evolution the PSC is useful because it is entirely consistent with the tenets of phylogenetic systematics, but it is also useful because it offers a simple and direct procedure for identifying fossil species that appears to be easy to operationalize: "In principle, a single ubiquitous apomorphy should be sufficient to diagnose a species under the PSC....." (Tattersall, 1992, p. 344). "When clearly identifiable hard-tissue autapomorphies are found consistently to discriminate between two fossil sister populations it is reasonable to conclude that speciation has intervened" (Tattersall, 1991, p. 80). Often of course, we do not have groups of fossils which are known from independent evidence to be representatives of 'sister populations',

and instead fossils are assigned to taxa because they possess traits that are assumed to be autapomorphies that differentiate sister taxa.

As discussed above phylogenetic species are not necessarily reproductively isolated from one another. The presence of an apomorphy in one of two closely related phylogenetic species is not proof that the two are permanently isolated and evolving independently of one another. Morphologically differentiated units need not be genetically independent units and the relationship between closely related phylogenetic species may be reticulate rather than hierarchical. If populations are not reproductively isolated, or if reproductive isolation is not permanent then the pattern of differentiation will most likely be transient; it will change as the pattern and degree of gene flow varies through time and the distinctions between populations may even disappear altogether.

Taxonomic units which are related to one another in a reticulate manner are inappropriate subjects for an analysis that assumes that all relationships are hierarchical, and for this reason it would seem that the PSC is a poor standard for identifying the units of a cladistic analysis, particularly for fossils where there is a time dimension. It has been claimed however, that although it may be the case that closely related extant species identified on the basis of morphological differentiation are not always genetically isolated and independent, fossil species identified by the same criteria will almost always correspond to genetically disjunct units (Kimbel, 1991; Tattersall, 1986, 1991, 1992) and therefore the PSC and character analysis can be used to detect and identify fossil species. Tattersall (1992) justifies this position with the argument that within extant primate species population differentiation is rarely reflected in 'hard-tissue morphology'. Therefore, groups of fossils which form minimally diagnosable units most likely correspond to species that are not only differentiated morphologically, but which are also reproductively isolated and genetically independent. "(W)here a morphological assemblage is readily and consistently identifiable on the basis of several characters (when, in other words it constitutes a 'morph', with its

own clearly recognizable *Gestalt*), it is highly likely to correspond at the very least to a genetically disjunct species, if not indeed to a (hopefully) monophyletic group of species....." (Tattersall, 1992, pp. 345).

According to Tattersall the relationship between differentiation and speciation in fossils is so strong that "where distinct morphs can readily be identified it would seem most productive to assume that they represent species unless there is compelling evidence to believe otherwise" (Tattersall, 1986, p. 168). In effect, Tattersall is proposing that when attempting to determine if variation in a collection of fossils is intra- or interspecific in nature the null hypothesis should be that more than one species is represented.

For different reasons Kimbel (1991; also Kimbel and Rak, 1993) has also taken the position that differentiated groups of fossils will almost always represent genetically isolated species. The basic premise of Kimbel's argument is that without reproductive isolation most population differentiation is ephemeral and therefore unlikely to be preserved in the fossil record:

> In the evolutionary long-term, intraspecific geographic differentiation, whether or not it is recognized taxonomically, is largely ephemeral (Mayr, 1970; Futuyma, 1987, 1989). The vast majority of local populations of polytypic species either become extinct or merge with parent populations as environments change and shift geographically over time and, as such, certainly would not be expected to leave behind much of a fossil record, let alone one with substantial time depth. Since significant morphological diversification among early hominids could hardly have proceeded without the geographical isolation and subsequent expansion of differentiated local populations, it is far more likely that the fossil record of this diversity reflects the successful establishment of new species than the maintenance of stable local populations through geological time (Kimbel, 1991, pp. 362-363).

Each of these arguments has its weaknesses. Tattersall's claim that primate populations that are morphologically differentiated but not genetically isolated are "difficult or impossible to diagnose on the basis of the hard parts which preserve in the fossil record" (Tattersall, 1992, p. 345) is based on an analysis of specific and subspecific differentiation in the genus *Lemur* (Tattersall, 1993). Lemurs, which are confined to a limited geographical area, may not be the most appropriate model of population and species differentiation in Plio-Pleisto-

cene *Homo*, a group which was widely distributed across eastern and southern Africa. A more appropriate comparative group would be modern humans, a species which has a wide geographical distribution and which is certainly more closely related to Plio-Pleistocene hominids than are lemurs. Morphologically modern humans are an extremely diverse species, and much of this differentiation is preserved in 'hard-tissue morphology' (see for example Bass, 1987, and references therein). Even within the limited geographic area of eastern and southern Africa modern human populations show strong morphological differentiation. Within this region pygmies, Bantu, Nilotic and Khoisan represent a wide range of diversity, much of which is preserved in their skeletal morphology.

Furthermore, it may well be the case, as Kimbel argues, that intraspecific population differentiation is almost always ephemeral, and the vast majority of differentiated populations may not leave behind much of a fossil record, or any fossil record for that matter. It does not follow however, that *all* of the diagnosable morphological differentiation seen in the hominid fossil record must be the result of speciation. It is practically tautological to use the PSC as a basis for species identification and then argue that all differentiation is the result of speciation; according to the PSC morphological differentiation *is* speciation. But if, as both Kimbel and Tattersall acknowledge, speciation also requires some degree of isolation then it becomes extremely unlikely that *all* diagnosable differentiation, or the appearance of *every* distinct morph in the hominid fossil record is the result of speciation because differentiation does not require isolation. Populations which are not reproductively isolated can and do become differentiated morphologically, and although the vast majority of such differentiation may not be preserved in the hominid fossil record it is extremely unlikely that none of it is. The claim that any particular instance of morphological differentiation in the hominid fossil record is the result of speciation is a hypothesis that needs to be tested, not an established fact on which to base reconstructions of evolutionary patterns.

At a more basic and fundamental level there is an additional problem with using the PSC and cladistic character analyses for detecting and recognizing species in the fossil record. Quite simply, character analyses cannot be used to identify species because the identification of species must precede character analyses. "For cladistic analysis, decisions about species necessarily precede knowledge about which character states are apomorphic" (Nixon and Wheeler, 1990, p. 217).

> In its requirement that a phylogenetic species be 'diagnosable by a unique combination of character states,' the PSC stipulates that every comparable individual of a phylogenetic species carry the entire complement of characters of that species. In contrast, if an attribute is fixed in one population but is a trait in another, or if two populations share a trait and differ only in its frequency of occurrence, or if an attribute is unique to one population but is not fixed, this trait cannot distinguish phylogenetic species.
>
> The character or characters that distinguish two phylogenetic species must differentiate every comparable individual of each species from every comparable individual of the other..... Phylogenetic species are diagnosable because their differences are fixed..... (Davis and Nixon, 1992, pp. 427-428).

Without prior, independent knowledge as to the number of species that might be present in a sample of fossils and which fossils might belong to which species there is no way of determining which features (if any) are fixed and apomorphic and which (if any) are polymorphic. In the absence of such knowledge using character analysis to detect species becomes an exercise in circular reasoning. At some period in time every derived trait must be polymorphic within populations and within a species. To group fossils together because they share a particular derived trait, and then to argue that that trait is an apomorphy because all of the specimens in that group possess the trait, and since they all possess that 'apomorphy' they must be a species separate from those specimens that lack the trait, is a completely circular argument. This is not say that character analysis is of no value, or that it cannot be used to provide diagnoses of fossil taxa, but it is not by itself an appropriate method for assessing the probability that multiple species are present in a collection of fossils.

Quantitative approaches to species discrimination

The second strategy that can be used to determine the likelihood that multiple species are represented in a collection of fossils is to use some quantitative measure of variation to compare variation in the fossils with variation in extant species that are closely related to the fossils. The reference species provide a measure of how much variation is reasonable for a single species. If variation in the fossils exceeds these limits then it can be inferred that more than one species is probably represented in the collection of fossils. This approach is more amenable to classical hypothesis testing than is character analysis. The null hypothesis is that the fossils represent only one species. If this is the case then variation in the fossils should fall within the limits of intraspecific variation seen in the reference species. The alternative hypothesis is that the fossils sample more than one species, in which case variation in the fossils *may* be greater that variation in the reference samples.

This procedure seems to offer a relatively simple way to ascertain if a collection of fossils represents one species or more than one species. When it is implemented however, it becomes apparent that it is not quite as simple and straightforward as it appears. There are for example, several important statistical issues that must be carefully addressed if the results are to be meaningful and valid. Among other things it is important to choose an appropriate measure of variation. In addition, if variation in the fossil sample is greater than variation in the reference samples there must be some way of determining if this difference is significant or if it is merely a chance result of sampling error. Discussion of these statistical issues is deferred to Chapter 8.

At a more basic and fundamental level this approach is limited in terms of what it can and cannot tell us about the number of species that might be in a sample of fossils and it is very important to have a clear understanding of these limitations. When this procedure is used as a test for multiple species in a collection of fossils the proper null hypothesis is that

the fossils represent only one species and therefore, assuming that uniformitarian principle are applicable, variation in the fossils should not exceed the limits of intraspecific variation seen in the reference species (Cope and Lacey, 1992; Kramer et al., 1995; Martin and Andrews, 1993; Turner and Chamberlain, 1989). Failure to reject the null hypothesis does not *prove* that the fossils comprise a single species, it merely indicates that the null hypothesis of a single species is not disproved. For example, Cope (1993) and Plavcan (1993) have both shown that for posterior dental dimensions mixed species samples of closely related extant primates may exhibit levels of variation that fall well within the ranges of intraspecific variation. As Martin and Andrews (1993, p. 400) note, "(i)f such morphologically homogenous samples were encountered in the fossil record, they would appear to represent a single species by available criteria, the implication being that a single-species interpretation can never be demonstrated conclusively in a fossil sample, it can only be falsified."

Thus, if an analysis based on variation of a particular trait or traits does not provide any justification for rejecting the null hypothesis of one species it does not definitively prove that only a single species is represented. It could be the case that an analysis using different traits may provide such evidence, or it may be that the metric differences between the species are simply not large enough to be detected in this way. On the other hand, if there are sufficient grounds for rejecting the null hypothesis then the different species must be described and individual specimens assigned to them. Beyond demonstrating that some of the differences between the species are size differences this method does not provide much guidance here, and it is at this point that character analysis may be informative. This quantitative approach has its own set of limitations, some of them rather serious, and it is really only a starting point for addressing questions of taxonomic heterogeneity.

CHAPTER 3

A NEW SPECIES OF THE GENUS *HOMO*

"Pre-*Zinjanthropus*"

By 1958, after 27 years of intermittent work, Louis and Mary Leakey had accumulated thousands of stone artifacts and faunal remains from the East African site of Olduvai Gorge. The collection of hominid remains was however, disappointingly small. The entire sample consisted of a late Upper Pleistocene burial, designated Olduvai Hominid (OH) 1, discovered in 1913 by Hans Reck (Oakley et al., 1977); two small cranial fragments derived from Lower Bed IV, designated OH 2, which according to Tobias (1991) may be a piece of frontal and a bit of parietal attributable to *Homo erectus*; and OH 3, a deciduous canine and extremely large deciduous molar from Upper Bed II, later classified as *Australopithecus boisei* (MD Leakey, 1971). Thus, the identity of the stone tool maker, known only from two deciduous teeth and two small, uninformative bits of a cranial vault, remained an enigma.

The turning point came in the summer of 1959 when Mary Leakey found a nearly complete cranium with a full maxillary dentition at the site of FLK in Middle Bed I. This was OH 5, the type specimen of *Zinjanthropus boisei* (LSB Leakey, 1959), later re-classified as *Australopithecus boisei* by Tobias (1967). Several weeks before the discovery of OH 5 however, one of the Leakeys' assistants came across a hominid molar embedded in a consolidated block of tuff in an exposure of Lower Bed I. This is OH 4, the first discovery of a fossil attributed to *Homo habilis*. The significance of OH 4 was completely eclipsed however, by the discovery of OH 5. Preliminary excavations at the '*Zinj* site' yielded large numbers of Oldowan tools, waste flakes and faunal remains, which suggested to its discoverers that the site represented 'a living floor of the Oldowan culture' (LSB Leakey, 1959, 1960). According to Louis Leakey (1959) OH 5 represented "one of the hominids who occupied the living site; who made and used the stone tools and who ate the animals" (p. 491). The Leakeys had at last found the maker and user of the Oldowan tools.

With the spectacular discovery of OH 5 the Leakeys received major financial support, allowing them to greatly expand operations at Olduvai. In 1960 extended excavations at FLK yielded three teeth, some fragments of parietal bone and a tibia and fibula. Originally all of these were ascribed to a single individual, designated OH 6, but it is currently believed that the tibia and fibula are from an older individual, now referred to as OH 35 (Tobias, 1991). Later, in the fall of 1960, Jonathan Leakey discovered a hominid tooth and a distal phalanx of the hand on the surface at the site of FLK North-North (FLK NN). Subsequent excavations resulted in the recovery of the remains of at least three individuals. The first of these (OH 7) consists of a juvenile mandible with a partial dentition, a nearly complete left parietal and portions of a right parietal, a number of cranial fragments and 21 bones of the hand, including several carpals and a number of phalanges. A partial left foot (OH 8) may represent a second individual if it is an adult (Tobias, 1991), or it may have belonged to the OH 7 juvenile (Sussman, 1983). Two left metatarsals (OH 43) which are definitely adult (Napier, 1962) represent a third (or second) individual and an unerupted upper molar (OH 45), originally associated with OH 7, represents a second juvenile much younger than OH 7 (Tobias, 1991). A radial shaft, a nearly complete clavicle and rib fragments were also found at the site, but because these all lack the epiphyseal regions their ages and therefore their relationship to the other hominid fossils is uncertain. All of these remains were found *in situ* in the same level, approximately 1½ feet *below* the *Zinjanthropus* horizon.

In his first published description of OH 7 Louis Leakey (1961a) noted that, with respect to a number of features of the vault and posterior dentition, the 'pre-*Zinjanthropus* child' differed from the australopithecines and *Zinjanthropus*, and seemed to represent a distinct type of early hominid. Leakey (1961a) described the parietals as:

> especially remarkable because, although they apparently belong to a young individual only twelve years old (or less), they are larger than those of *Zinjanthropus*. They are remarkably thin, and exhibit no sign of a sagittal crest or any marked temporal line. The lack of both these may, perhaps, be due in part to the youthful age. Nevertheless, these parietals suggest that we are dealing with a hominid with a larger brain capacity, as well as somewhat less specialized, than *Zinjanthropus*. (p. 649)

The premolars and molars were also described as 'remarkable' and quite unlike the posterior teeth of australopithecines. Leakey described the premolars and first molars of OH 7 as being longer mesiodistally and shorter buccolingually than those of australopithecines. In a subsequent paper he demonstrated that the posterior crown proportions of OH 7 were indeed distinctly different from those of the australopithecines (Leakey, 1961b). The crown length indices [(crown length/crown breadth) x 100] for the premolars and first molars of OH 7 fell beyond the ranges for the australopithecines. The index for both P_3's is 115.8, for the P_4's the indices are 104.0 and 104.7, and for the first molars the index is 117.0. For the combined *Australopithecus-'Paranthropus'* sample the indices were 76.0 - 91.9 for P_3, 61.1 - 91.1 for P_4 and 100.8 - 114.6 for M_1. Leakey concluded that the pre-*Zinjanthropus* juvenile was not an australopithecine, but rather 'a very remote and truly primitive ancestor of Homo'. Stone tools were also found at FLK NN, raising doubts in Leakey's mind with regard to who had made and used the Oldowan tools; was it *Zinjanthropus*, pre-*Zinjanthropus*, or both?

Shortly after the discovery of OH 5, the Leakeys invited Phillip Tobias to study and evaluate the OH 5 cranium, and as a result Tobias ended up describing and evaluating all of the cranial and dental material found at Olduvai between 1959 and 1972. Upon his first look at the OH 7 parietals it was immediately apparent to Tobias that they were greater in all dimensions (except for thickness) than the parietal bones of any known *A. africanus*, *A. robustus* or *A. boisei* crania. "One could not escape the uneasy feeling that a pair of parietals (i.e. OH 7) which were not only anteroposteriorly extensive, but laterally wide-spread, must have covered an endocranial cavity larger than any of the earlier hominids' then available. Just how much larger was the vexing question" (Tobias, 1991:19).

Tobias answered this vexing question by reconstructing the parietals and articulating them to form a biparietal arch. The biasterionic breadth of this reconstruction ($\approx$ 102 mm) was beyond the known australopithecine range and partial endocasts of the reconstructed

parietals yielded a mean volume of 363 cm^3 (Tobias, 1964a). Studies of complete fossil hominid endocasts showed that the partial endocast volumes of the parietals comprise 50 to 56% of the total endocast volume, and based on these ratios Tobias estimated that the total endocranial volume of OH 7 (uncorrected for age) was between 643 and 724 cm^3, with the most likely values ranging from 673 to 681 cm^3. At that time the estimated cranial capacities for australopithecines ranged from 435 - 530 cm^3 with a mean of 493 cm^3 if only adults were included in the sample, or 435 - 624 cm^3 with a mean of 511 cm^3 if Le Gros Clark's (1955) estimate of Taung's adult cranial capacity was included (Tobias, 1963). OH 7 had an estimated cranial capacity that was three or more standard deviations above the australopithecine mean (Tobias, 1965c) but considerably smaller than the smallest estimated endocranial volume for *Homo erectus* known at that time, which was 775 cm^3 (Weidenreich, 1943). Thus, with respect to cranial capacity, the Bed I juvenile was intermediate between the australopithecines and *Homo erectus*.

Tobias was also impressed by the proportions of the premolar and molar crowns of OH 7, and a comparison of OH 4 and OH 6 with OH 7 showed that all of these specimens possessed a distinctive buccolingual narrowing and mesiodistal elongation of the posterior teeth which set them apart from the australopithecines. Clearly, the pre-*Zinjanthropus* hominids of Olduvai were distinctly different from the robust australopithecines or *A. africanus* as it was then known, but they were certainly not *Homo erectus*. Although the cranial capacity of OH 7 was above the known australopithecine range it was also well below the range for *Homo erectus*. With respect to the shape of the posterior tooth crowns they were more similar to *Homo erectus* than *Australopithecus*, but in terms of overall size the posterior teeth were intermediate, being smaller than those of australopithecines, but not as small as those of *Homo erectus* (Tobias, 1965a, 1965b). The perplexing question was, what was pre-*Zinjanthropus*? Louis Leakey was convinced that it was not an australopithecine but rather an early form of *Homo*. Tobias however, was not so sure. Although at

times he felt that pre-*Zinjanthropus* must represent something new, at other times he inclined to the view that "the new juvenile bones should be regarded as simply widening our view of variability of *A. africanus* (Tobias, 1991, p. 21)." The gracile hominids of Olduvai might simply be a regional variant of *A. africanus*.

The postcranial bones from FLK and FLK NN had been given to Napier and his colleagues to study. According to Tobias (1991, p. 23) the postcranial bones "were far more *hominine* in structure and inferred function than was expected or surmised for *A. africanus* or other australopithecines", and both Napier (1962) and Day and Napier (1964) hinted at the possibility that the postcranial bones might be the remains of hominids which were contemporary with, but more advanced than, *Zinjanthropus*. The hand bones were described by Napier (1962) as being more primitive than the hand of a modern human in a number of respects, but functionally it is undoubtedly that of a hominid. The OH 7 hand is complete enough that Napier was able to determine that it possessed two of the three modifications necessary for a precision grip: the first carpometacarpal articulation indicates that the thumb was fully opposable, and the distal phalanges of the thumb and fingers are broad and spatulate. Because the metacarpal and proximal phalanx of the thumb are missing there is no way of determining if the third feature, a relatively long thumb, was present. However, Napier concluded that, whether or not it was fully capable of a precision grip, the OH 7 hand could easily have made the crude stone tools found in Bed I. Day and Napier's (1964) study of the OH 8 foot showed that it possesses all of the skeletal adaptations associated with bipedality. This was unexpected for a foot that was more than a million, and perhaps almost two million years old.

Thus, there were three independent lines of evidence, the large cranial capacity of OH 7, the long and narrow posterior teeth, and the modern morphology of the hand and foot, pointing to the existence of a gracile hominid at Olduvai which seemed to be too derived in the direction of *Homo* to be attributed to *Australopithecus*. For Tobias and Napier though

the final, conclusive evidence appeared in late 1963 when two fragmentary crania were found in Bed II. The first of these, OH 13, was discovered eroding out of lower Middle Bed II. This specimen consists of most of the mandible with all of the teeth, most of the maxilla, the majority of the occipital, much of the left temporal and parietal, portions of the left parietal and temporal, a few frontal fragments and about fifty other isolated cranial fragments which cannot be fit together (MD Leakey, 1971). The vault is very fragmentary and much less complete than suggested by the list of elements recovered (see for example Tobias, 1991, Fig. 17, p. 265). The second Bed II specimen is OH 16. This is derived from the base of Bed II and it represents a complete skull, including parts of the face and mandible and most of the teeth. It is, however, extremely fragmentary and incomplete because as the fragments weathered out of Bed II they were washed into a gully where they were trampled on and scattered by cattle. The reconstructed vault consists of 107 pieces of the frontal, parietals and occipital. There are an additional 1,500 fragments that cannot be fitted into the reconstruction (MD Leakey, 1971). The initial reconstructions of OH 13 and OH 16 indicated that the total endocranial volumes of both skulls were in excess of 600 cm^3 (Tobias 1991), and the teeth were also much more similar to OH 7 than to *Zinjanthropus* or the South African australopithecines (Leakey and Leakey, 1964).

The discovery of OH 13 and OH 16, and the combined evidence of the large cranial capacities, the long and narrow posterior teeth, and the modern morphology of the hand and foot, convinced Tobias and Napier that:

> we were dealing not with an isolated extreme variant of the australopithecines, but with a population four of whose major character-complexes -- those of brain, teeth, hand and foot--were remarkably like those of later members of the genus *Homo*. It was clearly a population that had moved away from the *A. africanus* pattern towards the *Homo* pattern of structure in all of the anatomical regions available for study and comparison (Tobias, 1991, pp. 24-25).

Furthermore, Tobias, Leakey and Napier believed that, with its larger brain and modern hand capable of a precision grip, the gracile Olduvai hominid was far more likely than *A. boisei* to have been the maker of the Oldowan Industry. With respect to their behavior (as it was

inferred) and their morphology the gracile Olduvai hominids were clearly derived in the direction of *Homo*. Or as Tobias (1991) put it more colorfully, "it seemed to us that our gracile Olduvai pygmies had stridden manfully across a generic boundary--from *Australopithecus* to *Homo*" (p. 30). The conclusion was that the gracile hominids of Olduvai should be classified as a new species of the genus *Homo*.

"A New Species of the Genus *Homo* from Olduvai Gorge"

The new species was christened and made its debut in 1964 in a letter to *Nature* authored by Leakey, Tobias and Napier. Leakey et al. chose to name their new species '*Homo habilis*', from the Latin meaning 'able, handy, mentally skillful, vigorous'. The name reflects their belief that the Oldowan stone tools had been produced by the 'Olduvai pygmies' rather than *A. boisei*.

In order to include *Homo habilis* within the genus *Homo* it was necessary to change the definition of the genus so that it was less restrictive. At that time the most recent and widely accepted definition of *Homo* was that of Le Gros Clark (1955). Leakey et al. made this definition more inclusive, primarily by expanding the acceptable range of cranial capacities from "a mean value of more than 1,000 cc" (Le Gros Clark, 1955, p. 79), to a range of "about 600 c.c. in earlier forms to more than 1,600 c.c. (Leakey et al., 1964, p. 7)." In the diagnosis of *Homo habilis* that followed the new species was described as having an average cranial capacity greater than that of australopithecines, but smaller than that of *Homo erectus*. The definition of *Homo habilis* also included diagnostic features of the postcranium (the hand and foot), mandible and cranium, and a number of dental traits, including buccolingual narrowing and mesiodistal elongation of the premolars and molars. In their diagnosis Leakey et al. did not list any features which were unique to *Homo habilis*. They chose rather to stress its transitional nature, emphasizing the combination of primitive (australopithecine-like) and advanced (*Homo erectus*-like) features and the features in which it is intermediate between the australopithecines and *Homo erectus*. For example, in terms

of overall size the molars are described as being "between the lower part of the range in *Australopithecus* and the upper part of the range in *Homo erectus*"; the sagittal curvature of the parietal bone ranges from "slight (within the hominine range) to moderate (within the australopithecine range)". A complete list of cranial, mandibular and dental features cited by Leakey et al. as being diagnostic of *Homo habilis* is provided in Table 1.

Leakey et al. designated OH 7 as the type specimen of *Homo habilis* . Olduvai hominids 13, 8, 6 and 4 were listed as paratypes and OH 16 was provisionally classified as *Homo habilis*. It was also proposed that several other African and perhaps even Asian fossil hominids might represent *Homo habilis*. Leakey et al. suggested that the South African '*Telanthropus capensis*' of Broom and Robinson (1949), later reclassified as *Homo erectus* by Robinson (1961), the Kanam mandibular fragment, the faciofrontal fragment from Yayo, Chad, and perhaps the cranial fragments and teeth from Ubeidiyah, were hominids which might ultimately prove to be *Homo habilis*.

"The Supposed Taxon, '*Homo habilis*'"

"Homo habilis", Homo erectus and *Australopithecus*

Leakey, Tobias and Napier and their new species drew a broadside of criticisms from some of the most prominent figures in paleoanthropology (e.g. Bielicki, 1966; Brace, 1969; Campbell, 1964a, 1964b; Howell, 1965; von Koenigswald, 1964, 1965; Le Gros Clark, 1964; Montagu, 1965; Oakley, 1964; Oakley and Campbell, 1964; Pilbeam and Simons, 1965; Robinson, 1965a, 1965b, 1966; Wolpoff, 1969). Among other things they were criticized for improperly naming their species, for revising the definition of the genus *Homo*, for creating a new species on the basis of a small and incomplete sample, for being too quick to announce their new species without having made thorough and careful comparative studies with other hominid fossils, for claiming that *Homo habilis* had made and used the Oldowan stone tools and implying that this justified its inclusion in the genus *Homo*, for including the post-cranial bones in their *Homo habilis* sample and their diagnosis of the

TABLE 1. Cranial, mandibular and dental features cited Leakey, Tobias and Napier (1964) as being diagnostic of Homo habilis

Cranial and mandibular features

1. Cranial capacity greater than *Australopithecus* but less than *Homo erectus*.
2. Slight to strongly expressed muscular markings.
3. Chin region retreating with slight to no development of a mental trigone.
4. Maxilla and mandible smaller than in *Australopithecus* and within the range for *Homo erectus* and *Homo sapiens*.
5. External sagittal curvature of the occipital less than in *Australopithecus* or *Homo erectus* and within the range for *Homo sapiens*.
6. External sagittal curvature of the parietal varies from slight to moderate.

Dental features

1. Incisors relatively large in comparison with those of both *Australopithecus* and *Homo erectus*.
2. Canines proportionally large relative to the premolars.
3. Premolars buccolingually narrower than *Australopithecus*, but within the range for Homo *erectus*.
4. Absolute molar dimensions are between the lower part of the australopithecine range and the upper part of the *Homo erectus* range.
5. Buccolingual narrowing and mesiodistal elongation of all teeth which is most pronounced in the lower premolars and molars.

species, for their failure to recognize that *Homo habilis* was no different from *A. africanus*, for their failure to recognize that *Homo habilis* was no different from *Homo erectus*, and for failing to recognize that their *Homo habilis* sample was a mixture of fossils which should be attributed to *A. africanus* and *Homo erectus*.

Some of these criticisms were relatively minor, but the most frequent, most persistent and most damaging criticism was that the gracile hominids of Olduvai were not representatives of a new species, but rather they were simply representatives of one or more of the hominid species already recognized and established. Exactly which species the *Homo habilis* fossils belonged to was a matter of disagreement. A few critics took the position that the Olduvai fossils should be placed in *Homo erectus* (Hughes, 1964, cited in Tobias 1991; Montagu, 1965). Montagu, for example, accepted the idea that *Homo habilis* was intermediate between australopithecines and pithecanthropines, but then went on to state that:

> ...to judge from the available data, it would be equally reasonable to conclude that *H. habilis* was, in fact, an early pithecanthropine. There is nothing in the published data that would not conform to the requirements of the latter hypothesis. Applying Occam's razor, *H. habilis* could perhaps more appropriately be regarded as an early representative of *Homo erectus*. Such a ligature can allow for the slight morphological differences that may exist between them, without separating them into distinct species. (Montagu, 1965, p. 918)

At the opposite extreme, and in far greater numbers, were those who argued that *Homo habilis* was really only an australopithecine, or that the fossils from Bed I were australopithecines and the fossils from Bed II *Homo erectus*. For example:

> .....the details of Leakey's fossils thus far published appear to provide no sound reason for distinguishing them from the genus *Australopithecus*..... the similarities of Leakey's fossils with known specimens of *Australopithecus* are so remarkable, and the differences from known fossil remains of *Homo* are so great, that their relegation to the former genus can hardly be in doubt. (Le Gros Clark, 1964, p. 49)

> The differences between the East African "habilis" (sensu lato) fossils and the South African forms *(A. africanus)* are not sufficient, in my opinion, to justify specific distinction: they can be accounted for by the geographical and chronological diversity in this single lineage. (Campbell, 1973, p. 198)

> The East African form (*Homo habilis*) is a lightly built, small-brained, bipedal hominid, very similar to *A. africanus* although the latter has a somewhat smaller brain and shows slight differences in the dentition. There are two possible interpretations..... these samples could be subspecies, albeit rather different ones, within the same species, and such differences as do exist could be due to the fact that *H. habilis* is geologically younger and hence more evolved than *A. africanus*. Alternatively, these two samples could belong to two separate but related lineages, roughly equivalent perhaps to two similar but geographically separated baboon lineages. .....provisionally, I should like to group *africanus* and *habilis* in the same genus, *Australopithecus*. I think it possible that they are members of a single species, which would therefore be called *Australopithecus africanus*, and which would have two subspecies: *A. a. africanus* in South Africa and *A. a. habilis* in East Africa. (Pilbeam 1970, pp. 161-162)

> .....there seems to be no good reason for separating early species of the genera *Australopithecus* and *Homo* on grounds of differences in cranial volume. None of the crania from the Transvaal breccias or from Olduvai Beds I and II indicate volumes outside the range now known among the single species of living gorilla, and all these crania are distinctly smaller than those of *Homo erectus*. The teeth and mandible of *H. habilis* from Olduvai Bed I FLK NN I do not differ greatly from specimens of *A. africanus* in shape or morphology. The molars are similar in size and shape to those of *A. africanus* from Sterkfontein (Robinson, 1956). The premolars of *H. habilis* are somewhat narrower than those of the South African forms; but shape, as well as size, of teeth is known to vary greatly in all modern primates, including man, and this seems to be a relatively unimportant character on which to base generic and specific separation of the two forms..... *H. habilis* and *A. africanus* may represent nothing more than two variant populations within the same widespread species..... (Pilbeam and Simons, 1965, pp. 250-251)

Many paleoanthropologists believed that the Bed I fossils should be classified as *A. africanus* and the Bed II fossils as *Homo erectus*. This may be due in part to the fact that at that time the Bed I hominid sites had been dated by K/Ar to between 1.6 and 1.9 Ma whereas samples from the top of Bed I yielded dates of 1.23 Ma (Leakey, Evernden and Curtis, 1961). Thus Bed I appeared to represent perhaps 500 - 700 ka, and the Bed II fossils were generally believed to be ca. 1 Ma and contemporary with the Indonesian *Homo erectus* fossils from Sangiran (e.g. Campbell, 1973; LSB Leakey, 1965; Pilbeam and Simons, 1965; Tobias, 1965a; Tobias and von Koenigswald 1965). Furthermore, the Bed II fossils had been described as being more advanced or 'hominized' than the Bed I fossils, particularly with respect to the smaller size of the posterior teeth and the size and morphology of the mandibular corpus (Tobias, 1965a, 1965b; Tobias and von Koenigswald 1965). If the Bed II hominids were no more advanced than the Bed I hominids it would imply hundreds of

thousands of years of morphological stasis and the possibility that two species of Homo were contemporary with each other, *Homo habilis* in Africa and *Homo erectus* in Asia. At that time many paleoanthropologists were committed to a gradual, unilineal interpretation of human evolution. Within this conceptual framework, it was only logical to view the Bed II hominids as more advanced than the Bed I specimens and classify them as *Homo erectus*.

The most inveterate and formidable critic of *Homo habilis* was J. T. Robinson (1965a, 1965b, 1966), who firmly maintained that it was not a valid taxon. Robinson (1965a, 1965b) believed that Leakey et al. had failed to demonstrate that their *Homo habilis* sample represented a taxon different from the hominid taxa that had already been recognized. He began his assault on *Homo habilis* by showing that the length/breadth indices of OH 7 and OH 4 fall within or only slightly outside the ranges for *A. africanus*, and concluded from this that buccolingual narrowing and mesiodistal elongation of the lower premolars and molars did not distinguish *Homo habilis* from *A. africanus*. He then claimed that, in any case, the length/breadth indices were irrelevant because, "it is very clear that this character has very low phyletic valence and is thus virtually useless for taxonomic purposes in hominids" (Robinson, 1965b, p. 404). The evidence of cranial capacity was dismissed with little discussion, "The endocranial capacity of *H. 'habilis'* appears, on the scanty and indirect evidence available, to have differed little from that of the australopithecines with a range overlapping that of the latter substantially" (Robinson, 1965a:122).

Robinson's (1965a) comparisons of the Bed I and Bed II hominids with *Australopithecus* and *'Telanthropus'* led him to conclude that the Bed I fossils are more like *Australopithecus*, and the Bed II specimens are more like *Homo erectus*, than the Bed I fossils are like those from Bed II. Although he did view the gracile hominids from Bed I as a transitional stage linking *Australopithecus* and *Homo erectus* he still believed them to be nothing more than advanced australopithecines which ought to be classified as *A. africanus*, whereas the Bed II fossils were early members of *Homo erectus*. Robinson (1965a) concluded that:

> clearly no new species name is needed: the situation is simply one common in palaeontology when specimens are found which link two already existing taxa. Creating a new taxon here is no solution; the two taxa between which the new one falls are already so similar that insufficient morphological distance exists between them to justify the insertion of another species. (p. 123)

Robinson (1965a, 1966) proposed that perhaps *Australopithecus* (which for him included only one species, *A. africanus*) should be included in the genus *Homo*. His rationale for this was the idea that the series *Australopithecus - Homo habilis - Homo erectus* represents a single lineage whose members all share a distinctive adaptive pattern in which unique behavioral traits, such as making and using tools, complex social structure and language, are most important. Sinking *Australopithecus* into *Homo* was further justified on the grounds that, "the sequence appears to contain no major morphological changes, no major shifts in evolutionary direction and did not occupy a very long geological time" (Robinson 1966, p. 958). Classifying *A. africanus* as *Homo* would also have had the effect of minimizing the differences between *A. africanus* and *Homo erectus*, providing support for Robinson's claim that the morphological distance between them was not great enough to warrant classifying the transitional Bed I specimens as a separate species.

Culture, competitive exclusion and the single-species hypothesis

An additional obstacle to the acceptance of *Homo habilis* was created by the single species hypothesis, which was advocated primarily by Brace (1965) and Wolpoff (1968, 1971, 1973). The basic premise of this hypothesis was the idea that only one hominid species could possibly exist at any particular point in time. According to Wolpoff culture was the most important adaptive mechanism and the adaptive niche of all hominid species, even the earliest. "Because of cultural adaptation, all hominid species occupy the same, extremely broad, adaptive niche" (Wolpoff, 1971, p. 601). However, Wolpoff claimed that, because culture enlarges the range of environments that can be exploited, allopatric hominid species would inevitably expand, become sympatric, and since they occupy the same niche, compete with one another. This competition would lead to the extinction of one of these

species, as predicted by the principle of competitive exclusion. The ultimate result would be, "the continued survival of only one hominid lineage" (Wolpoff, 1971, p. 601). In other words, two hominid species cannot coexist in time, and all fossil hominids must be members of a single, unbranching lineage. Variation between contemporary hominids must be intraspecific in nature, reflecting sexual dimorphism, polytypism or simply intra-populational variation. It cannot be interspecific variation.

In order to defend the single-species hypothesis it was necessary to minimize the differences between the gracile Olduvai hominids and the australopithecines and/or *Homo erectus*. Consequently, Wolpoff (1969, 1970) attempted to prove that there was no justification for separating *Homo habilis* from *Australopithecus* by demonstrating that if the cranial capacity of OH 7 is included in a sample of endocranial volumes for the South African representatives of '*Homo africanus*' the value for the former is not excessively large. The mean of this combined sample is 521 cm^3, with a standard deviation of 67 and a coefficient of variation (CV) of 12.9 (Wolpoff, 1969). According to Wolpoff the cranial capacity of OH 7 is only 2.03 standard deviations above this mean and the CV is not unusually large. Based on these results he concluded that in terms of cranial capacity, "Olduvai hominid 7 cannot be justifiably removed from *Homo africanus*" and therefore, "the specimens attributed to (Bed I) '*Homo habilis*' would better be regarded as East African representatives of *Homo africanus*" (Wolpoff, 1969, p. 182).

According to Tobias (1991), the most 'damaging onslaught' on *Homo habilis* was a paper coauthored by Brace (Brace, et al., 1973), the other major advocate of the single species hypothesis. In this paper, which had the rather telling title 'Tooth measurements and the rejection of the taxon "*Homo habilis*"', the authors used graphs and univariate and multivariate analyses to compare the teeth of OH 7, OH 13 and OH 16 with those of *Homo erectus* and *Australopithecus*. Interestingly, these comparisons involved tooth crown areas only. The authors attempted to justify this by arguing that crown areas are more informa-

tive because, "these appear to compensate in part for the genotype to phenotype translation error evident in either the mesial-distal or buccal-lingual measurements taken singly" (p. 54). However, because they used only crown areas they overlooked the differences in crown proportions emphasized by Leakey et al. (1964). The graphic comparisons and univariate statistics showed that, with respect to tooth crown areas, OH 7 and OH 16 could not be distinguished from *A. africanus*, whereas OH 13 could not be distinguished from *Homo erectus*. Discriminant analyses yielded identical results: OH 7 was classified as an australopithecine, and OH 13 as *Homo erectus*. These results led Brace et al. to the conclusion that, "(s)ince the taxon '*Homo habilis*' is without a type specimen, a usable paratype or any unequivocal referred material, it is an empty taxon inadequately proposed and should be formally sunk" (p. 66).

Further Discoveries in East Africa

Homo habilis was vigorously defended by Leakey (1964, 1966) and Tobias (1964b, 1965a, 1965b, 1966), but the debate carried on in the literature probably contributed little to its eventual recognition as a valid species. Until the middle to late 1970's most paleoanthropologists were, at best, equivocal about this taxon. This skepticism and ambiguity is apparent in the fact that references to *Homo habilis* were almost always qualified with quotation marks as, for example, *Homo 'habilis'*, *'Homo' habilis* or *'Homo habilis'*. One factor which probably did have a significant role in the acceptance of *Homo habilis* was the appearance of a new generation of paleoanthropologists who were generally not as strongly committed to a gradualistic, uniform, unilineal theory of human evolution as their predecessors. More importantly, during the late 1960's and early 1970's, the size and quality of the early *Homo* sample increased dramatically, partly as the result of continuing work at Olduvai Gorge, but primarily as the result of work at East Lake Rudolf (now Lake Turkana) in Kenya, and the Omo Basin in Ethiopia. The discovery at East Rudolf of a robust australopithecine contemporary with *Homo erectus* disproved the single species hypothesis, and as the

number of early *Homo* specimens increased it became evident that the earliest members of the genus *Homo* were different enough from *Australopithecus* and *Homo erectus* to warrant classification as a separate species.

Olduvai Hominid 24

The most complete *Homo habilis* cranium from Olduvai Gorge is OH 24. The skull was found in 1968, in a gully about 300 m east of FLK I. It was found on the surface, but the calcareous matrix in which it was embedded is identical with concretions formed around fossils derived from a stratum between the Bed I lavas and Tuff IB (MD Leakey et al., 1971; Tobias, 1991). Except for OH 4, all of the other hominid fossils from Olduvai were found above Tuff IB, thus OH 24 and OH 4 are the earliest hominids in the Olduvai sequence. The skull was found completely embedded in a block of matrix, and it had been very badly crushed and distorted. After extraction and reconstruction it was found that much of the cranial vault and face is relatively complete and intact, although there are still some areas which are slightly distorted or cannot be reconstructed (Clarke, 1991).

In the first published description of OH 24 (MD Leakey et al., 1971) it was described as definitely belonging to the genus *Homo*. The authors cited a number of features, for example, a relatively large endocranial capacity (which they estimated to be greater than 560 cm^3), reduced postorbital constriction, expansion of the parietal region of the brain and corresponding lateral expansion of the parietals, posterior projection of the occipital, a deep and narrow mandibular fossa, and a slender temporal zygomatic process, as features in which OH 24 differs from australopithecines and resembles early *Homo*. They also noted that with respect to a few cranial and dental features, most notably the small size of the posterior teeth OH 24 resembles OH 13 from Bed II. Nevertheless, because the skull also retains some primitive features, they were equivocal about whether or not OH 24 should be attributed to *Homo habilis*. It was suggested that, if OH 24 is *Homo habilis*, it and OH 13 may be females, whereas the more megadont OH 16 and OH 7 might represent males.

Others have been less equivocal about the issue, and OH 24 has been attributed to *Homo habilis* by a number of workers (e.g. Chamberlain and Wood, 1987; Groves, 1989; Groves and Mazák, 1975; Howell, 1978; Tobias, 1972, 1991; Wolpoff, 1980; Wood, 1991, 1992, 1993).

Regardless of how it was classified, the discovery of OH 24 made it much more difficult to refer the Bed II fossils to an early form of *Homo erectus*. The fact that OH 24, one of the earliest early *Homo* fossils at Olduvai, and OH 13, one of the latest, both have small posterior teeth demonstrates that for the latter this characteristic is not an advanced or *Homo erectus*-like feature. For the Olduvai *Homo habilis* fossils variation in tooth size cannot be ascribed to an evolutionary trend in the direction of *Homo erectus*. Rather, it must be due to some other factor, such as sexual dimorphism or simply normal variation within a population.

Omo

Between 1967 and 1976 intensive work by a joint French-American team resulted in the collection of a large number of hominid fossils from Plio-Pleistocene deposits in the Lower Omo Valley of Ethiopia. The fossil-bearing sequence at Omo consists of a number of formations, two of which, the Usno and Shungura formations, have yielded the remains of late Pliocene and early Pleistocene hominids. Within these two formations there are numerous tuffs which have been dated radiometrically and which serve as markers for stratigraphic correlations. As a result the Plio-Pleistocene hominids are well defined chronologically and are known to span the time period between 3.1 and approximately 1.3 Ma (Feibel et al., 1989). The hominid sample is relatively large, there are 247 specimens, but unfortunately it is also very fragmentary and the great majority of specimens (87%) are isolated teeth (Coppens, 1980). Nevertheless, at least four taxa have been recognized in this sample: *A.* aff. *africanus*, *A. boisei*, *Homo habilis*, and *Homo erectus* (Coppens, 1980; Howell and Coppens, 1976).

All of the fossils referred to *Homo habilis* are derived from the Shungura Formation, from strata that are between 2.1 and 1.75 Ma (Howell and Coppens, 1976; Feibel et al., 1989). The collection is small, and consists of one fragmentary skull with teeth and six isolated molars and premolars whose attribution to *Homo habilis* is based on their size and crown proportions (Coppens, 1980).

The skull, Omo L 894-1 is derived from Shungura Submember G-28 and therefore dates to between 1.9 and 1.88 Ma (Boaz and Howell, 1977; Feibel et al., 1989). It consists of 50 cranial fragments and all of the posterior maxillary teeth except the left P^4. The dimension of the teeth have been described by Boaz and Howell (1977) as being 'virtually identical' with those of OH 24. According to the same authors the cranium, which is 30 to 40% complete, is undoubtedly that of a gracile hominid with similarities to both *A. africanus* and early *Homo*, but the resemblances to the latter are the most notable. For example, although the vault is too incomplete to allow for an accurate determination of the endocranial volume, it must have been substantially greater than in *Australopithecus*, the mastoid region also does not show the extensive pneumatization characteristic of *A. africanus*, the face is less prognathic, and the mandibular fossa is deep and narrow. Boaz and Howell felt that Omo L 894-1 most closely resembles OH 24, OH 13 and Sangiran 4. Consequently, they suggested that it should be attributed to *Homo habilis* or *Homo modjokertensis*. In their conclusion they stated that:

> There is an increasing body of evidence that indicates the presence of a pre-*erectus* *Homo* species in the Old World tropics and sub-tropics in the range of time of approximately between 2.3 and 1.5 m.y. B. P. But without further and more definite data on provenance, particularly from Indonesia, any taxonomic assignation to this early *Homo* taxon would be premature. (p. 106)

Boaz and Howell avoided directly attributing Omo L 894-1 to *Homo modjokertensis* or *Homo habilis* because they felt that the former species name might have priority over the latter, but only a year later Howell (1978) attributed it to the latter species.

Early *Homo* at East Rudolf

Some of the most significant fossil discoveries of the 1970's came from the area of East Lake Rudolf (also known as Lake Turkana or Koobi Fora) in Northern Kenya. Among other things the hominid fossils discovered at Koobi Fora effectively refuted the single species hypothesis by proving that *A. boisei* and *Homo* had coexisted, and the fossils from Koobi Fora also demonstrated the existence of an early, pre-*erectus* species of *Homo*.

The sequence of exposed strata at East Turkana is collectively referred to as the Koobi Fora Formation. It comprises eight members which together span the time period between 4.3 and 0.6 Ma (Brown and Feibel, 1986). The great majority of hominid fossils are derived from three of these members; from oldest to most recent these are the Burgi, KBS and Okote members which collectively represent the late Pliocene and early Pleistocene, between 1.9 and 1.5 Ma (Feibel et al., 1989).

The Koobi Fora Research Project began in 1968. During the first two years the only hominid fossils found were those of robust australopithecines. Evidence of the genus *Homo* did not appear until 1970 when a gracile mandible with relatively small posterior teeth was found in the KBS Member. This mandible was very different from the robust australopithecine mandibles that had been found in the same stratigraphic level and Richard Leakey (1971) provisionally referred it to the genus *Homo*, although he did not attribute it to any particular species. Subsequently, several additional mandibles attributed to *Homo* were discovered and in 1975 a well-preserved, nearly complete *Homo erectus* cranium, KNM-ER 3733, was found in the KBS member, slightly below the stratigraphic level in which the robust australopithecine cranium, KNM-ER 406 had been found (Leakey and Walker, 1976). These two specimens could not possibly be members of the same species, and the discovery of KNM-ER 3733 convincingly disproved the single species hypothesis by demonstrating that robust australopithecines and *Homo* had coexisted in both time and space.

Beginning in 1972 a remarkable collection of fossils were also found below the KBS Member, in the Upper Burgi Member. Some of the specimens from the Upper Burgi Member were undoubtedly robust australopithecines, but some cranial, mandibular and postcranial specimens indicated the presence of an early species of *Homo* as well. Of all the hominids found below the KBS Tuff KNM-ER 1470, a nearly complete cranium, is undoubtedly the most significant. This skull was reconstructed from more than 150 fragments which were found weathering out of the slope of a gully (Leakey et al., 1978). The reconstructed skull is fairly complete and is preserved as two main parts: the calvarium, which is missing the cranial base; and the face, which is missing the lateral portions of both maxillae and all but the frontal processes of the zygomatics. The face and vault join at nasion and there is also some contact along the lateral wall of the left orbit.

KNM-ER 1470 shows an interesting combination of features which had not been seen in any known form of hominid. In the first published description of the skull Leakey (1973a) noted that there is only moderate postorbital constriction and the parietals are expanded so that their lateral walls are nearly vertical. These features indicate a relatively large endocranial volume, which Leakey estimated to be greater than 800 cm^3. Holloway (1978) later estimated it to be 752 cm^3. KNM-ER 1470 exhibits a number of other characteristics which are typical of *Homo*, but in some respects, particularly in the face and maxilla, it resembles *A. boisei*. For example, the face is large relative to the vault (Walker, 1976) and the palate is broad with a nearly straight labial border, but the size of alveoli for the anterior teeth indicate that they were large (Leakey, 1973a).

According to Leakey (1973a) the large endocranial volume and the morphology of the vault indicate that KNM-ER 1470 ought to be included in the genus *Homo*, but because of its unusual combination of features he did not believe that it could be attributed to any of the known species of *Homo*. Because it lacks the specialized features characteristic of *Homo erectus* Leakey felt it was probably not an early representative of that species. The

only other species of *Homo* to which it could be referred was *Homo habilis*, but the estimated cranial capacity of KNM-ER 1470 was more than a 100 cm^3 greater than the endocranial volume of OH 7, the largest of the *Homo habilis* specimens from Olduvai Gorge. Therefore, according to Leakey KNM-ER 1470 was neither *Homo erectus* nor *Homo habilis*, but rather than creating and naming a new species he simply proposed that it should be attributed to *Homo* sp. indet.

Leakey's unwillingness to refer KNM-ER 1470 to *Homo habilis* or *Homo erectus* was due in large part to the fact that the KBS Tuff, which marks the bottom of the KBS Member, had been dated by K/Ar to 2.6 Ma. (Fitch and Miller, 1970). Therefore KNM-ER 1470, which had been found 35 m below this tuff, was believed to be on the order of 2.9 Ma. old (Leakey, 1973a). If this date were correct KNM-ER 1470 would be at least a million, and perhaps as much as two million years older than OH 9 from Olduvai Bed II, the oldest *Homo erectus* fossil known at that time. It would also make KNM-ER 1470 at least 700,000 and perhaps more than a million years older than the *Homo habilis* fossils from Olduvai, all of which have cranial capacities that are more than 100 cm^3 less than the 800 cm^3 estimated for KNM-ER 1470. It is now known that Fitch and Miller's date of 2.6 Ma. for the KBS Tuff is incorrect. More recent K/Ar, $^{40}Ar/^{39}Ar$ and fission track ages for the KBS Tuff securely place it at 1.88 ± 0.02 Ma. (Gleadow, 1980; McDougall, 1985; McDougall et al., 1980).

Following the discovery of KNM-ER 1470 two additional large-brained hominids resembling this specimen were found below the KBS Tuff. The first of these is KNM-ER 1590, which consists of a fragmentary cranium and many of the maxillary teeth of a juvenile. Even though most of the parietals and parts of the frontal are preserved KNM-ER 1590 is far too incomplete to allow for any reliable estimation of cranial capacity, but it is evident that the braincase was relatively large and the endocranial volume was as large or larger than that of KNM-ER 1470 (Holloway, 1978; Leakey, 1974). In 1975, a third cranium, KNM-ER 3732, was found below the KBS Tuff. This is a partial vault which retains the left orbit and

much of the frontal and parietals. It is slightly smaller than KNM-ER 1470, but according to Leakey (1976b) the two are 'strikingly similar'.

In 1973 two rather enigmatic cranial specimens, which might represent early *Homo*, were discovered *in situ* in the Upper Burgi Member. The first of these is KNM-ER 1805 which was found above the KBS Tuff and just below the Okote Tuff. This specimen is preserved in three parts. The first part consists of the cranial vault, which is missing the supraorbital region and most of the cranial base. The second portion consists of the lower part of the face and the palate, which is complete and includes nearly all of the maxillary teeth. The third part is the corpus of the mandible which is missing most of the tooth crowns. Unfortunately, there is no articulation between the facial fragment and the cranial vault.

KNM-ER 1805 is like KNM-ER 1470 in that it shows an unusual combination of features. Leakey (1974) estimated that the cranial capacity was between 600 and 700 cm^3. Holloway (1978) later determined that it is actually 582 cm^3. There is only moderate postorbital constriction, and KNM-ER 1805 actually shows less postorbital constriction than KNM-ER 1470; according to Wood (1991) minimum frontal breadth is 81 mm for the latter and 88 mm for the former. The mandible and teeth are also small, and in these features, as well as in the large cranial capacity and reduced postorbital constriction KNM-ER 1805 resembles *Homo*. However, the skull also bears low, but distinct parasagittal crests which diverge posteriorly and run into a well-developed nuchal crest. In his initial description of this specimen Leakey (1974) did not refer it to any species or genus.

The second cranium, KNM-ER 1813, was found below the KBS Tuff during the 1973 field season. This cranium is relatively complete, lacking only part of the left side of the face, the zygomatic arches, most of the sphenoid, part of the left occipital and some of the maxillary tooth crowns. KNM-ER 1813 has the smallest cranial capacity of any of the non-robust australopithecine hominids from the Upper Burgi member. Leakey (1974) estimated

the cranial capacity to be approximately 500 cm^3, which is close to the Holloway's (1978) estimate of 509 cm^3. As suggested by the relatively small cranial capacity KNM-ER 1813 is much smaller than KNM-ER 1470, showing greater postorbital constriction and smaller vault dimensions. In these respects it is more similar to *A. africanus* than are KNM-ER 1470, 1590, 1805 or 3732. The resemblance to *A. africanus* was noted by Leakey (1974, 1976a, 1979; Leakey et al, 1978) who suggested that it might be a gracile hominid with close affinities to that species.

In addition to the crania a number of mandibles and postcranial elements attributed to *Homo* were also found below the KBS Tuff. The mandibles can be sorted into two groups on the basis of size. Of the large mandibles KNM-ER 1802 is the best preserved and most complete. The corpus of this specimen is relatively large and robust, overlapping in size with A. *boisei* (Wood, 1991) and the posterior teeth are also relatively large (Day et al., 1976). However, the teeth and mandible lack the specialized features characteristic of australopithecines and Leakey (1974) suggested that it ought to be, "considered as belonging to the same genus and species and KNM-ER 1470 and 1590" (p. 655).

Of the smaller mandibles the most complete and informative specimens are KNM-ER 1501, 1503 and 1507. These three mandibles were all initially attributed to the genus *Homo* by Leakey (1973b) because they, "are gracile and show a morphology similar to that seen on the *Homo* mandible from Ileret, KNM-ER 992" (Leakey, 1973b, p. 172). However, Leakey later changed his opinion and attributed KNM-ER 1501, 1503 and 1507, along with KNM-ER 1813, to a "small-brained gracile hominid (which) appears to have its strongest affinities with the South African species *Australopithecus africanus*" (Leakey et al., 1978, p. 89).

The most taxonomically informative postcranial remains are a single partial innominate, KNM-ER 3228, and a number of fragmentary and a few relatively complete femora. The innominate is distinctly different from the australopithecine innominates from Sterkfontein

and Swartkrans (Leakey, 1976a). In some features KNM-ER 3228 most closely resembles the *Homo erectus* innominate OH 28, and in other respects it resembles modern humans. According to Leakey (1976a) its "(r)esemblances to OH 28 from Olduvai Gorge and the essentially modern appearance of this fossil require that it be attributed to *Homo*".

A sample of relatively complete and partial femora were also recovered below the KBS Tuff. These can be sorted into two groups. The first group possess the distinctive features characteristic of australopithecines, such as a relatively small, hemispherical femoral head, a long, anteroposteriorly compressed femoral neck, and a more acute neck-shaft angle. The second group of femora exhibit features diagnostic of *Homo*. In these specimens the femoral head is larger and forms a more complete sphere, the neck-shaft angle is more obtuse and the femoral neck is shorter and rounder in cross section. The postcranial elements cannot be directly associated with any of the cranial remains, but the discovery of postcranial elements below the KBS Tuff which exhibit so many distinctive features characteristic of *Homo* is strong additional evidence for the existence of an early species of *Homo* in the Upper Burgi Member.

Since their discovery the taxonomy of the non-robust hominids from the Upper Burgi Member has been a matter of disagreement and changing interpretations. The debate has revolved around several questions. The first and most basic question concerns the number of species represented in this sample. Some paleoanthropologists have taken the position that these fossils most likely represent a single species, *Homo habilis* (e.g. Cronin et al., 1981; Kimbel et al., 1984; Howell, 1978; Miller, 1991, 1994; Tobias, 1991; Wolpoff, 1980). On the other hand, there are those who feel that at least two species of gracile hominids are present in the Upper Burgi Member. If this is the case then there is a second question to be addressed; namely, to which species should these fossils be attributed? Most commonly it is argued that there are two species of *Homo*, one of which is *Homo habilis* (e.g. Lieberman et al., 1988; Rightmire, 1993; Stringer, 1986; Wood, 1991, 1993),

but it is also possible that there is only one species of *Homo* and the second gracile hominid is an australopithecine (e.g. Leakey, 1979; Leakey et al., 1978). If there are multiple species present there is a final issue to be resolved, and this concerns which fossils should be attributed to which species. On this question there is a surprising lack of agreement among those who argue for multiple species. For example, Wood (1991, 1993) has assigned KNM-ER 1813 and 1805 to *Homo habilis* and KNM-ER 1470, 1590 and 3732 to a second species of *Homo*, whereas Rightmire (1993) has attributed KNM-ER 1470, 1590 and 3732 to *Homo habilis* and KNM-ER 1813 and 1805 to a different species of early *Homo*, and Leakey (1974; 1979), who initially believed that KNM-ER 1470 was an early species of *Homo* which was neither *Homo erectus* nor *Homo habilis*, has suggested that KNM-ER 1470, 1590, 1802 and 3732 are *Homo habilis* and KNM-ER 1813 a gracile australopithecine. Although there is still a great deal of disagreement concerning the number and identity of the species present and the taxonomy of the individual specimens, all of the gracile hominids from the Upper Burgi Member have been designated , sometimes individually and sometimes collectively, as *Homo habilis*.

Early *Homo* in South Africa

Telanthropus capensis

The first discovery of a fossil hominid which was contemporaneous with australopithecines and which could reasonably be attributed to the genus *Homo* occurred in South Africa, eleven years before OH 7 was found at Olduvai Gorge. In 1949 Robert Broom and J. T. Robinson recovered two mandibles at the site of Swartkrans which, "cannot belong to the ape-man, (i.e. *A. robustus*) and are apparently human" (Broom and Robinson, 1952, p. 110). The first mandible, SK 15, is relatively complete. It was found in a small pocket of breccia within a solution cavity. The breccia in this pocket was darker than the pink breccia in which all of the '*Paranthropus*' remains had been found, and Broom and Robinson (1949, 1952) were certain that SK 15 must be younger than the hominid fossils from the main

breccia, although they felt that it might not be much younger. They named this 'new type of man' *'Telanthropus capensis'* which they regarded as an "intermediate between one of the ape-men and true man" (Broom and Robinson, 1949, p. 322).

The second specimen, SK 45, is a fragment of a right mandibular corpus. This fossil was found in the pink breccia and it was therefore definitely contemporaneous with *A. robustus* (Broom and Robinson, 1950, 1952). Broom and Robinson (1950) did not refer SK 45 to *Telanthropus*, stating only that, "(a)t present we can merely say that the jaw is manifestly not that of *Paranthropus crassidens*, and that it appears to be the jaw of an early type of man" (p. 154).

After Broom's death Robinson (1953) reversed himself, claiming that the pocket of breccia in which SK 15 was found was coeval with the pink breccia. He believed that SK 15 and SK 45, and the maxilla SK 80 which had also been found in the pink breccia, were contemporary with one another and could all be ascribed to *Telanthropus capensis*. His comparison of these three fossils with *Paranthropus*, *'Plesianthropus'*, *Pithecanthropus* and modern human specimens reaffirmed his earlier opinion concerning the intermediate nature of *Telanthropus*:

> The present evidence seems to allow of no other conclusion than that *Telanthropus* represents a stage between that of the australopithecines and the known euhominids. The similarities between *Telanthropus* on the one hand and either of the other groups on the other seem too detailed and too numerous to allow of any other conclusion. (p.487)

Robinson changed his opinion again in 1961 when he formally proposed that *Telanthropus* was an invalid taxon which should be sunk and the specimens attributed to it classified as *Homo erectus*.

In 1969 Ronald Clarke, while studying the australopithecine fossils at the Transvaal Museum, noticed that the face of the cranium SK 847 from Swartkrans, which had been catalogued as *Paranthropus*, appeared to be very different from the other robust australopithecine faces from that site. Clarke thought that SK 847 might in fact be *Telanthropus*,

and in comparing the posterior palate of SK 847 with the anterior palatal fragment SK 80 he found that the two articulated perfectly. Furthermore, he was able to articulate SK 847 with SK 846b, a relatively complete left temporal. The SK 45 mandibular fragment may also belongs to this individual (Tobias, 1978), which is now referred to as SK 847.

In their analysis of SK 847 Clarke, Howell and Brain (1970) confirmed Robinson's (1953) appraisal of the *Homo*-like features in the palate and mandible of *Telanthropus* and identified a number of definitive *Homo* features in the face and vault as well. The most salient of these are: prominent nasal bones which project well beyond the maxilla, thick and pronounced supraorbital tori and a broad supraorbital sulcus, a more vertical orientation of the frontal behind the supratoral sulcus, reduced postorbital constriction and temporal lines which are poorly defined and well separated. In these features SK 847 differs from robust and gracile australopithecines and resembles *Homo*.

Clarke subsequently came across two other early *Homo* specimens in the collection of fossil hominids from Swartkrans. The first of these is SK 27, a juvenile cranium which had been classified as *Paranthropus* by Broom and Robinson (1952). This cranium had a cranial capacity of approximately 700 cm^3, large anterior teeth and relatively small, narrow molars (Clarke, 1977b). These features align SK 27 with *Homo* rather than *Paranthropus*. The third specimen consists only of two heavily worn upper premolars which possess several features diagnostic of *Homo* (Clarke, 1977b). Because these three early *Homo* fossils were approximately contemporary with one another it is likely that they are all members of the same species.

Excavations at Swartkrans carried out between 1965 and 1986 resulted in the recovery many more hominid fossils, and also enabled Brain (1988; Brain et al., 1988) to determine that there are five fossil bearing depositional units at this site which are of distinctly different ages. Hominid remains representing *A. robustus* and *Homo* were found in the first two depositional units, Members 1 and 2, whereas only *A. robustus* fossils have been

positively identified in Member 3 (Brain, 1988; Grine, 1989). All of the hominid fossils found by Broom and Robinson were derived from 'Hanging Remnant' of Member 1, except for the SK 15 mandible which is from Member 2 (Brain, 1976). The *Homo* fossils recovered during the new excavations consist of isolated teeth and a partial mandible, which collectively represent five or six individuals (Grine, 1989).

The Swartkrans hominids can only be dated by faunal correlation. According to Vrba (1982, 1985) the bovids indicate a date of between 1.8 and 1.6 Ma for Member 1. This is consistent with Delson's (1984, 1988) analysis of the cercopithecid fossils, which suggest that Member 1 is between 1.9 and 1.65 Ma. The dates for the more recent Members 2 and 3 are much less certain (Brain, 1988; Delson, 1988).

Early *Homo* at Sterkfontein

In 1956 indirect evidence of early *Homo* was also found at the site of Sterkfontein. In that year excavation of the *in situ* breccia west of the Type Site resulted in the recovery of 58 stone artifacts (Mason, 1957; Robinson, 1957). In the following year excavations in this area, which became known as the Extension Site, yielded many more stone artifacts, a single bone implement and a small sample of hominid teeth (Robinson, 1959, 1962). This work also resulted in a much clearer picture of the stratigraphy at Sterkfontein and Robinson (1962) was able to identify three distinct breccias at the site: the pink Lower Breccia in which almost all of the australopithecine fossils had been found; the Middle Breccia in which the stone artifacts had been found, and an Upper Breccia. Robinson was also able to determine that the Extension Site breccia is more recent than that of the Type Site (Robinson, 1957, 1962). Although Robinson (1962) was certain that all of the teeth from the Middle Breccia represented *A. africanus* he did not believe that the stone artifacts had been made and used by australopithecines, preferring instead to attribute them to *Telanthropus*. Tobias (1965b) however, noted some resemblances between the teeth from the Middle Breccia and the *Homo habilis* teeth from Olduvai, which led him to cautiously propose that

the hominid from the Middle Breccia might represent something more advanced than an australopithecine:

> I do not, for a moment, believe this proves *H. habilis* is represented in the Middle Breccia. All I claim is that evidence of these 3 teeth *suggests*, however slightly, the presence, in the Middle Breccia, of another hominid. Only the recovery of further remains from the Middle Breccia can confirm or refute this suggestion. (p. 409)

Tobias' suggestion was eventually confirmed when renewed excavations at Sterkfontein led to the discovery of new hominid fossils in the Middle Breccia. At that time the full stratigraphic sequence of the Sterkfontein Formation was also defined, and as a result the Lower, Middle and Upper Breccias were renamed Members 4, 5 and 6, respectively (Partridge, 1978).

The most significant hominid specimen from Member 5 is an incomplete skull, designated Stw 53. The skull is fragmentary but a great deal of it is preserved. Much of the face is present, including the palate with all of the posterior teeth from the right side. A large part of the frontal, and portions of the sphenoid, parietal, occipital and right temporal bones are also preserved (Hughes and Tobias, 1977; Tobias, 1978). A number of definitive features align Stw 53 with early *Homo* rather than *Australopithecus*. Among other things, postorbital constriction is not as pronounced as it is in the latter and the temporal lines are well separated; these two features suggest a moderately large cranial capacity. The browridges are thin, but somewhat prominent, and the morphology of this region is reminiscent of OH 16 and OH 24. In the morphology of the nasal bones, which are elevated rather than flat, and in the morphology of the nasal floor and subnasal maxilla Stw 53 resembles early *Homo* and is quite different from *A. robustus* or *A. africanus* (Hughes and Tobias, 1977; Tobias, 1978). Furthermore, the heavily worn teeth show a well-marked helicoidal pattern of attrition. According to Tobias (1980) this wear pattern is never seen in australopithecines but is very common in early *Homo*.

A variety of approaches have been used in an attempt to determine the ages of the Sterkfontein deposits, but the only dependable dates are based on faunal correlation.

According to Vrba (1982) the bovid remains indicate that Sterkfontein Member 5 is, "close in time to SK1 (Swartkrans Member 1), but perhaps marginally later" (p. 735). Thus, in age Member 5 falls somewhere 1.8 and 1.6 Ma. The cercopithecid fossils are consistent with this age estimate (Delson, 1984), whereas Partridge (1985, 1986) believes that the faunal and the archeological evidence indicate that Member 5 dates to the more recent end of this time span. Recently Schwarcz et al. (1994) attempted to use ESR to determine the age of bovid teeth from Sterkfontein Member 4. The distribution of ages which they obtained was bimodal, with the larger peak at 2.37 ± 0.29 Ma and the smaller peak at 1.72 ± 0.31 Ma. The authors suggested that the second age peak could be due to the presence of teeth from Member 5. If this is the case the dates derived from ESR are consistent with the dates indicated by the fauna, but they must be considered as tentative, at best.

The taxonomy of early South African *Homo*

The taxonomy of the early *Homo* fossils from South Africa is an issue that remains to be resolved. It is most often the case that when specific attributions are made SK 847 is referred to *Homo erectus* and Stw 53 to *Homo habilis*, but these are far from universally accepted. Often these specimens are simply referred to as early *Homo*, or an early form of *Homo* with affinities to *Homo erectus* (SK 847), or affinities to *Homo habilis* (Stw 53).

In their description of Stw 53 Hughes and Tobias (1977) avoided directly referring it to any particular species, noting that the skull exhibits:

> a preponderance of individual features aligning it with early *Homo* species. It clearly has very little in common with *H. erectus* and would seem to be far too small-brained, thin-skulled and mildly crested to be accommodated in that taxon. On the other hand, the total picture indicates a strong affinity with the small-skulled, moderately brained and structurally distinctive *H. habilis*. Stw 53 differs from *A. africanus* in much the same way as does the roughly contemporary, pygmoid, brainy *H. habilis* of East Africa..... (p. 312)

The authors then concluded that Stw 53 belonged either to *Homo habilis* or to a closely related species, which they referred to as, *'Homo* aff. *habilis'*.

A reconstruction of Stw 53 by Clarke (who had also been responsible for the restoration of OH 24) has done much to clarify the question of its taxonomic affinities. Clarke's reconstruction appears to be almost identical to OH 24 (see for example: Clarke, 1985, fig. 1; or Tobias, 1991, fig. 3). Tobias (1978) had already noted a marked similarity between the two fossils in the morphology of the frontal, but Clarke's reconstruction shows that they resemble one another in many other areas as well, such as in the curvature and height of the parietals, in the shape and curvature of the occipital, in the size of the face and in the degree of alveolar prognathism. The similarities between the two are so pronounced that many paleoanthropologists now consider Stw 53 to be a South African representative of *Homo habilis*.

Clarke et al. (1970) also carefully refrained from referring SK 847 to a particular species. They did note some resemblances between SK 847 and *Homo erectus*, but concluded that it should be treated as *Homo* sp. indet. until a detailed study of the cranium could be carried out and pending the discovery of more fossil material. Clarke and Howell (1972) observed that in some respects the Swartkrans cranium resembles OH 13 and they suggested that perhaps, "SK. 847 and the other 'Telanthropus' hominid fossils may ultimately prove to be conspecific with Olduvai H. 13" (p. 333).

The detailed study of SK 847 referred to by Clarke and Howell became Clarke's doctoral dissertation (Clarke, 1977a, cited in Tobias, 1978). Clarke found that, although SK 847 shows strong affinities with *Homo erectus*, it also resembles East African fossils attributed to *Homo habilis*, and he was therefore unable to reach any conclusion about how it ought to be classified. In spite of its similarities to *Homo erectus* Howell (1978) included SK 847, along with fossils such as OH 24, KNM-ER 1813 and KNM-ER 1470, in *Homo habilis*. Clarke (1985) however, eventually reached the opposite conclusion after his comparisons of SK 847 with KNM-ER 3733 convinced him that the former is a South African representative of early *Homo erectus*, "the *erectus*-like morphology of the frontal bone (which is not seen

in any of the *Homo habilis* crania) plus the remarkable overall similarity to 3733 convinces me that 847 must now be classified as an early *Homo erectus*" (p. 173).

Generally, SK 847 is considered to be *Homo erectus* and Stw 53 *Homo habilis.* However, a recent paper by Grine et al. (1993) suggests that these two fossils may be members of the same species. Grine and his colleagues used randomization methods to determine the significance of the taxonomic distances between SK 847 and Stw 53, KNM-ER 1813, KNM-ER 3733 and WT 15000. Their results suggest that the two South African crania could be derived from the same population, and are more closely related to one another than either is to any of the East African specimens. Principal coordinates analysis of the distances between the fossils indicates that the two South African specimens show the closest affinity to KNM-ER 1813, which has been attributed to *Homo habilis*, rather than to KNM-ER 3733 or WT 15000, which have been attributed to *Homo erectus* (or *Homo ergaster*). These results suggest to the authors that the two South African fossils are members of the same species and should be attributed to *Homo habilis*, or possibly a new species of *Homo*. However, the distance statistic used by Grine et al., the average taxonomic distance of Sneath and Sokal (1973), may not be the best measure of taxonomic affinity because the variables, in this case cranial measurements, are assumed to be uncorrelated with one another.

Homo habilis Comes of Age

As the sample of early *Homo* fossils increased in size and completeness it became apparent that Leakey, Tobias and Napier had been justified in classifying the earliest members of the genus *Homo* as a separate species, and by the middle to late 1970's there was a general consensus among paleoanthropologists concerning early *Homo* and *Homo habilis*. The fossil evidence showed that in Africa *Homo erectus* had been preceded by an earlier, more primitive hominid which was too advanced to be an australopithecine. This early form of *Homo* bridged the gap between *Homo erectus* and *A. africanus*, but was

distinctly different from both. The differences were considered to be significant enough to warrant assigning these fossils to a separate species and there was sufficient justification for classifying some, and perhaps all of them as *Homo habilis*. An excellent example of this change in perception is F. Clark Howell, who in 1965, expressed a great deal of skepticism about the validity of *Homo habilis*. At that time Howell agreed with Robinson in arguing that the Bed I gracile hominids were an East African form of *A. africanus* and the Bed II specimens an early form of *Homo erectus*. In 1978 however, Howell recognized *Homo habilis* as a valid species, attributing specimens from Olduvai (OH 7, 13, 16 and 24), East Rudolf (KNM-ER 1470, 1590, 1813, and 3732), Omo (Omo L 894-1) and South Africa (SK 847) to this taxon. Howell concluded that, although some questions concerning *Homo habilis* were unresolved, it was nevertheless a valid, legitimate species:

> I consider, however, that these early hominids, which are not yet *H. erectus* and which significantly diverge in total morphological pattern of craniofacial, dental and postcranial morphology from *A. africanus*, represent a distinct taxon. It is a valid species in its own right..... (Howell, 1978, p.193)

CHAPTER 4

HOW MANY SPECIES OF EARLY *HOMO*?

The discoveries made in the late 1960's and early 1970's at Koobi Fora and Olduvai Gorge demonstrated that Leakey, Tobias and Napier had been right. *Homo erectus* had been preceded by a gracile, relatively large-brained hominid that was not an australopithecine. The gracile, pre-*erectus* hominids from Koobi Fora convinced all but the most hardened critics that *Homo habilis* was a legitimate species and these specimens, along with OH 24, have all been attributed to *Homo habilis*, either collectively or individually, by many paleoanthropologists. But as these fossils were discovered and described it became apparent that there is a great deal of variability, both in size and shape, within the collection of fossils referred to *Homo habilis*. So much so that some workers began to suspect that they might actually represent more than one species. There have been a number of attempts to prove this, but none of these has been able to provide unequivocal evidence of multiple species. Consequently many paleoanthropologists today have taken the position that the variation seen in *Homo habilis* reflects nothing more than sexual dimorphism, polytypism and perhaps evolutionary change through time, within a single species. On the other hand however, there is a growing body of evidence that suggests that there were at least two species of gracile hominids in East Africa during the Plio-Pleistocene. One of these species is *Homo habilis*. The identity of the second is unclear. It has been suggested that it may be a gracile australopithecine, but among those who argue for multiple species the general opinion seems to be that it is a second species of *Homo*. Thus, more than thirty years after its christening and debut the integrity of *Homo habilis* continues to be the subject of controversy.

The purpose of this chapter is to review the arguments for and against multiple species of early *Homo*. The possibility that *Homo habilis* may represent more than one species has been raised repeatedly in a variety of contexts. Often such suggestions are made tangen-

tially, within the framework of research whose primary focus is a different issue altogether, such as hominid phylogeny, the evolution of particular morphological features, or descriptions and reviews of fossils from particular localities. In this context authors sometimes note ways in which the differences between early *Homo* specimens appear to be inconsistent with their being members of the same species. Some of these differences suggest that some specimens may actually represent a species of *Australopithecus* rather than a second species of early *Homo*. There are also a number of studies which have attempted to systematically prove that *Homo habilis* represents multiple species. Here the focus is on demonstrating that the magnitude of variation is too great, or the pattern of variation is too different within *Homo habilis* to allow for the reasonable attribution of all of these specimens to a single species. Often these studies also attempt to classify individual fossils. For the sake of simplicity and clarity the former works are discussed first. Thus, the first section of this chapter is a review of the evidence and opinions on the taxonomy and affinities of the most complete and informative *Homo habilis* crania: OH 24 and KNM-ER 1470, 1805 and 1813. These are the specimens that are compared with one another in this dissertation. This is followed by a review of the more systematic studies that have attempted to prove the existence of multiple species of early *Homo*. Although this dissertation is concerned only with the cranial and dental evidence for multiple species the postcranial evidence is also relevant, and this is briefly discussed here. The chapter closes with a review of the arguments and evidence for *Homo habilis* as a single species.

The Taxonomy of the Gracile Plio-Pleistocene Hominids

Olduvai Hominid 24

This cranium was first described in 1971 by Mary Leakey, Ronald Clarke and Louis Leakey. In their summary Leakey and her colleagues came to the conclusion that "(b)eyond doubt, the new specimen represents the genus *Homo* as defined by Leakey, Tobias and

Napier and differs fundamentally from the australopithecines." The authors list a suite of features, such as reduced postorbital constriction, lateral expansion of the parietals and a relatively large cranial capacity (which they estimated to be minimally 560 cm^3), to support their attribution. They also noted that in many respects OH 24 resembles the *Homo habilis* fossils from Olduvai Gorge, especially OH 13 from Bed II, and yet they were hesitant to assign it to *Homo habilis* because they felt that, "it differs in some respects from the type of *H. habilis* from Bed I" (p. 308). The most salient differences are in the small size of the posterior teeth and the form of the lambdoid suture. In OH 24 (and OH 13) the lambdoid suture forms an inverted V, whereas in OH 7 and 16 it follows a low, wide arch. The differences in the size of the teeth could simply represent sexual dimorphism, "it is possible that Olduvai H. 13 and H. 24 represent females of *Homo habilis* with the type and O.H. 16 representing males" (p. 312), but the differences in the form of the lambdoid suture suggested to the authors the possibility of 'taxonomic variation.'

It was not long before someone pointed out that in some respects OH 24 resembles a gracile australopithecine. The author of an anonymous commentary in *Nature* (1971) argued that the small estimated cranial capacity and the shape of the face, which is concave in profile, point to australopithecine affinities for OH 24. According to this author:

> The dished face is a composite feature of considerable evolutionary significance and its absence in later hominines represents a diminution of the teeth and jaws, with reduced prognathism in the lower part of the face and emergence of the nose. The profile line drawing..... clearly demonstrates the dished face of Olduvai Hominid 24 and serves to emphasize its overall similarity with the undoubted australopithecines from South Africa. (p. 295)

In a later letter to *Nature* (Anonymous, 1972) the same author reiterated his claim that OH 24 was an australopithecine, citing as evidence its 'near identity' with MLD 6 from Makapansgat, South Africa:

> Although MLD 6 is a fragmentary specimen, the preserved portion of its central facial area shows a near identity with the comparable portions on OH 24, not only in size and shape but in detailed morphology. Moreover, the teeth which can be compared, PM^4 and M^1, although showing different

> degrees of wear, are extremely similar in their measurements, relative sizes and general conformation. (p. 469)

Other workers have also found similarities between OH 24 and *A. africanus*, particularly in the region of the mid-face. Franciscus and Trinkaus (1988) have shown that the unique projecting, external nose of modern humans is related to a suite of skeletal features, such as nasal bone convexity, an internasal angle, eversion of the lateral nasal aperture, prominence and anterior positioning of the anterior nasal spine and an acute angle of the subnasal alveolar clivus, which appears with the emergence of *Homo erectus* ca. 1.6 million years ago. The australopithecines lack these specializations, and retain the primitive hominoid morphology for this region. (i.e. the nasal bones are flat, the internasal suture lies on the same coronal plane as the nasomaxillary suture so there is no internasal angle, the inferior portions of the frontal process of the maxilla and the lateral walls of the piriform aperture are not significantly everted, the anterior nasal spine is only weakly developed and not visible in lateral view and the angle between the nasoalveolar clivus and the floor of the nasal aperture is not acute). For OH 24 Franciscus and Trinkaus find that the nasal bones are flat and lack an internasal angle, the lateral nasal aperture is not everted, and although there is a nasal spine present it is not visible in lateral view. Thus OH 24 retains the more primitive, flat, non-projecting nasal morphology characteristic of australopithecines and apes and lacks the derived pattern seen in later members of the genus *Homo*. This morphological pattern is not found in all early *Homo* faces. KNM-ER 1470 shows, where the morphology is preserved, the modern human pattern.

Olson (1978), using cladistic methods, also identified similarities between OH 24 and *Australopithecus* in certain features of the nasal bones as well as in the morphology of the mastoid processes. According to Olson the combination of shared derived and primitive features seen in OH 24 is identical to the pattern seen in *A. africanus* (which he refers to as "*Homo africanus*"). Olson claims that are no features that distinguish OH 24 from the

South African *"H. africanus"* fossils and he argues that it belongs to the same species as the gracile australopithecines from Sterkfontein and Makapansgatt.

The face of OH 24 also strongly resembles australopithecines in its pronounced subnasal prognathism (Bilsborough and Wood, 1988) and in the lateral profile of the face, which is 'folded' along a bilateral line extending from the lateral margin of one orbit to the other. According to Rak (1983) this latter feature is characteristic of *A. africanus* but is not found in early *Homo*. Another feature which aligns OH 24 with *Australopithecus* is the antero-inferiorly sloping malar (Bilsborough and Wood, 1988). Of the crania attributed to early *Homo* only OH 24 possesses this feature, which it shares with australopithecines. The remaining early *Homo* crania resemble *Homo erectus* in having a vertical or backward sloping malar (Bilsborough and Wood, 1988).

The resemblances between OH 24 and *A. africanus* are so pronounced that Wolpoff (1994), who is a staunch defender of *Homo habilis* as a single species, has described it as the most australopithecine-like *Homo habilis* cranium. Many of the resemblances cited by Wolpoff are features of the mid-face identified by Franciscus and Trinkaus (1988) and discussed above, but he adds the presence of anterior pillars bordering the nasal aperture and depression of the frontal behind the supraorbital tori to the list of similarities between OH 24 and *A. africanus*. Wolpoff does not feel that the resemblances are so great that OH 24 should be classified as an australopithecine, and he identifies a number of other features, such as the larger cranial capacity, the short and broad cranial base, the anterior position of the foramen magnum and vertical orientation of the malar, in which it differs from *A. africanus* and resembles the *Homo habilis* crania from Koobi Fora. According to Wolpoff (1994) the resemblances between OH 24 and *A. africanus* are to be expected in a species that is transitional between *Australopithecus* and *Homo erectus* and OH 24 merely extends the range of variation seen in *Homo habilis*. Like Wolpoff, Dean and Wood (1981, 1982) see some australopithecine-like features in the cranial base morphology of OH 24, but they

also find that in other features it resembles *Homo erectus* and modern *Homo sapiens*. In their opinion the overall resemblance to the latter is stronger.

The endocast appears to provide stronger evidence for classifying OH 24 as *Homo* rather than *Australopithecus*. Tobias (1987, 1991) estimates that the cranial capacity is 594 cm^3, a value which is well outside the known australopithecine range. Holloway (1978) however, has suggested that even Tobias' (1972) preliminary estimate of 567 cm^3 may be a significant overestimate of the true value. The relatively large cranial capacity by itself is suggestive of *Homo*. More importantly however, OH 24 endocasts resembles *Homo* in its proportions. The differences between australopithecines and *Homo* in the endocast are due to a slight increase in height and a marked increase in breadth, but no change in length (Tobias 1987, 1991). The endocast of OH 24 shows the lateral expansion of the brain characteristic of *Homo*. The biparietal width is exaggerated due to the distortion and flattening of the vault, but even when this distortion is taken into account the endocast is still broader across the parietals, temporal and frontal regions than the endocasts of australopithecines (Tobias 1987, 1991). Because of this broadening the outline of the frontal region is squarish, and in this respect it resembles KNM-ER 1470 (Falk, 1983; Tobias 1987, 1991). In addition the endocast suggests that OH 24 had a well-developed Broca's area and Wernicke's area. According to Tobias (1987, 1991) the OH 24 endocast shows stronger development of the inferior parietal lobule (which includes Wernicke's area) than is characteristic of australopithecine endocasts.

Another distinctive feature which aligns OH 24 with *Homo* is its helicoidal dental plane. According to Tobias (1980) this is a feature that is characteristic of *Homo* but never seen in South African australopithecines. In *Homo* the wear of the mandibular dentition is greatest on the buccal side of the anterior posterior teeth and on the lingual side of the most posterior teeth with the transition occurring somewhere along the molars. In contrast, in *Australopithecus* there is a uniform upward slope toward the palate (i.e. wear is heaviest on

the buccal side and the occlusal surface slopes toward the cheek side). The helicoidal plane is caused by differences in arch width between the molar teeth in the upper and lower dental arcades which Tobias (1980) relates to the overall reduction in the m-d length of the 2nd and 3rd molars in *Homo*. Even though the degree of dental wear is slight, a helicoidal occlusal plane is 'unmistakably present' in the maxillary teeth of OH 24 (Tobias, 1980). Since one of the features that distinguishes *Australopithecus* from *Homo* is reduction of the posterior teeth, Tobias (1980, 1991) regards this as further evidence that OH 24 belongs in the genus *Homo* rather than *Australopithecus*.

KNM-ER 1470

In his initial assessment of KNM-ER 1470 Leakey (1973a) acknowledged that:

> (t)he taxonomic status of the material is not absolutely clear..... The endo-cranial capacity and the morphology of the calvaria of KNM-ER 1470 are characters that suggest inclusion within the genus *Homo*, but the maxilla and facial region are unlike those of any known form of hominid. Only the flat fronted wide palate is suggestive of *Australopithecus*, but its extreme shortening and its shallow nature cannot be matched in existing collections representing this genus (p. 450).

This statement neatly sums up the debate over the taxonomy of KNM-ER 1470. The large cranial capacity and the size, shape and morphology of the cranial vault all support its inclusion in the genus *Homo*, but the large, broad and orthognathic face with its wide palate and deep, anteriorly placed and anteriorly sloping malars are suggestive of *Australopithecus*, particularly the robust species. Most often the cranium is referred to early *Homo*, or *Homo habilis*, but many workers have noted the resemblances to *Australopithecus* evident in the face, and Walker (1981; Walker and Leakey, 1978) has gone so far as to refer it to that genus.

Walker (1976) provided a list of features in which KNM-ER 1470 resembles australopithecines: the face is large relative to the vault, in the degree of postorbital constriction it is intermediate between *Australopithecus* and *Homo*, although cranial capacity is above the *Australopithecus* range but at the very low end of the *Homo* range,

the vault is thin-walled and has a bell-shaped profile when seen from the rear, maximum cranial breadth is at the level of the supramastoid crest and the mandibular fossae are transversely elongated and partially overhung by the zygomatic process of the temporal. He concluded, ".....on the criteria given here it can be seen that several features that seem to be constantly found in *Australopithecus* are found in this cranium, not the least of which is the relative proportion of the facial skeleton to the neurocranium. I am not suggesting that on this evidence 1470 is an *Australopithecus*, but I am arguing for caution....." (p. 489). In a later paper Walker (1981) was less cautious, and proposed that even though KNM-ER 1470, and the other large crania from the Lower Member, represent a population antecedent to the *Homo erectus* populations in the Upper Member, "the crania from the Lower Member are best placed in the genus *Australopithecus*, their major differences from *A. africanus* being probably only of size" (p. 213). Olson (1978), based on the shape and configuration of the nasal bones and the morphology of the mastoid region of the temporal has also classified KNM-ER 1470, as well as KNM-ER 1805 and 1813, as "*Homo* (=*Australopithecus*) *africanus*".

The results of a multivariate analysis of Plio-Pleistocene hominid faces by Bilsborough and Wood (1988) suggest that the facial similarities between KNM-ER 1470 and *Australopithecus* are superficial and reflect little more than an anteriorly placed malar and *m. masseter*. Although they found that in some aspects of facial morphology KNM-ER 1470 resembles *Australopithecus* they also demonstrated that there are significant differences in the shape of the face that suggest that KNM-ER 1470 is not an australopithecine. In their canonical variates analysis the face of KNM-ER 1470 occupies an intermediate position between the two morphological patterns seen in Plio-Pleistocene hominids. The first pattern is represented in its most extreme form by the large, probably male, *A. boisei* specimens. *A. robustus* and *A. africanus* represent successively less extreme forms of this pattern. At the other end of the continuum are the small, gracile early *Homo* specimens, OH 24 and

KNM-ER 1813. KNM-ER 1470 occupies an intermediate position between the australopithecines and small early *Homo*.

For most paleoanthropologists the large cranial capacity, which Holloway (1978) has estimated to be 752 cm^3, seems to be sufficient evidence that KNM-ER 1470 represents *Homo* and not *Australopithecus*. But the morphology of the endocast, particularly the frontal lobes, also supports its attribution to *Homo*. Holloway (1978) has described the frontal lobe as being 'very reminiscent of *Homo erectus*'. According to Falk (1983) the sulcal pattern of the endocast is completely human, not ape-like, and it also shows the lateral expansion of the frontal and parietal lobes characteristic of *Homo* (Falk, 1983; Tobias 1991). Falk (1983) feels that the KNM-ER 1470 endocast represents the earliest human-like sulcal pattern in the human fossil record. In particular she claims that the external morphology in and around Broca's area appears normal for a modern human, and concludes on this basis that KNM-ER 1470 had probably been capable of speech.

For KNM-ER 1470 the nasal morphology resembles, where it is preserved, the modern human pattern with convex nasal bones and an internasal angle, and some eversion of the lateral walls of the nasal aperture (Franciscus and Trinkaus, 1988). Wood (1985) has also argued that, although the vault of KNM-ER 1470 may show an overall resemblance to *Australopithecus*, the resemblances are more apparent than real. It appears that for a number of features in the vault, face and cranial based KNM-ER 1470 does not resemble *Australopithecus*, but rather is derived in the direction of *Homo* (Wood, 1985, table 3, p. 212). According to Wood (1985) KNM-ER 1470 resembles *Homo*, rather than *Australopithecus*, in its larger overall size, greater contribution of the occipital to the sagittal arc, wider parietals, more orthognathic face (which is even more orthognathic than in *A. robustus* or *A. boisei*), lack of prominence of glabella, everted nasal margins, shorter and wider cranial base, wider sphenoid, more coronal axes of the petrous temporals and more anterior position of porion. Thus, although it may be the case that most

paleoanthropologists who refer KNM-ER 1470 to the genus *Homo* do so on the basis of cranial capacity, there are many other features which support this attribution.

KNM-ER 1805

The one word that is used most often to describe KNM-ER 1805 is 'enigmatic'. Wolpoff (1994) has described it as a 'taxonomic nightmare' because this specimen exhibits a combination of features which are not seen on any other hominid skull, making it extremely difficult to identify the its true affinities. The estimated cranial capacity is 582 cm^3 (Holloway, 1978), there is only a moderate degree of postorbital constriction, the lateral walls of the vault are nearly vertical and the mandible and teeth are relatively small. These are all features which support its attribution to the genus *Homo*. But the cranium also possesses low parasagittal crests which nearly touch in the midline and which merge into well developed compound temporonuchal crests, the cranial base is extensively pneumatized making the skull very wide across the base, and although the mandible is small it is also quite robust (Chamberlain and Wood, 1985; Day et al., 1976; Wood, 1991). In the first published description of KNM-ER 1805 Leakey (1974) did not know what to make of it. He described it as 'undoubtedly important', but also 'enigmatic'. In the conclusion to this paper Leakey suggested that there were three hominid taxa represented at Koobi Fora: a robust australopithecine, a gracile australopithecine, and *Homo*. He did not attribute KNM-ER 1805 to any of these. In a later paper he proposed that it belonged to a species of 'late-surviving small *Australopithecus*' (Leakey and Walker, 1980).

Leakey is not the only worker who sees evidence of australopithecine affinities in KNM-ER 1805. The morphology of the endocast, nasal region, cranial base, some aspects of the teeth and the pattern of ectocranial cresting, all support the attribution to *Australopithecus*. Falk (1983) has shown that the endocast of KNM-ER 1805 is very similar to those of pongids and australopithecines. In terms of its overall shape it is quite primitive, with relatively narrow frontal lobes (an ape-like feature) and the parietal lobes lack the lateral

expansion seen in KNM-ER 1470. The sulcal pattern of the inferior frontal lobe is also distinctly australopithecine-like (Falk, 1983). Holloway (1978, 1983) also considers it to be an australopithecine. The morphology of the nasal region, where it is preserved, resembles *Australopithecus* as well. It appears that the nasal bones were flat and that there was no internasal angle, there is no true anterior nasal spine present, and although there is some eversion of the lateral walls of the nasal aperture it is not pronounced (Franciscus and Trinkaus, 1988). In the areas of the nasal region that are preserved KNM-ER 1805, unlike KNM-ER 1470, retains the primitive australopithecine/ape morphological pattern.

The most unusual feature of KNM-ER 1805 is the presence of parasagittal and temporonuchal (T/N) crests and these are also suggestive of australopithecine affinities. Sagittal and T/N crests are characteristic of male *A. boisei* skulls, but in *A. boisei* the sagittal crest begins well anterior to bregma (Kimbel et al., 1984) whereas in KNM-ER 1805 the parasagittal crests begin approximately 30 mm behind bregma (Wood, 1991). In *A. afarensis* T/N crests are present, and sagittal crests are sometimes also found. In those *A. afarensis* crania that do have a sagittal crest there is variation in the location of its origin; in some specimens it begins anterior to bregma and in others it begins posterior to bregma (Wolpoff, 1996).

A metrical study by Dean and Wood (1982) found that the cranial base of KNM-ER 1805 most closely resembles those of robust australopithecines and in the dentition there are also several features that suggest affinities to these hominids. Tobias (1980) in fact, identified KNM-ER 1805 as *A. boisei*, based on the fact that the mesiodistal (m-d) diameter of the M^3 is greater than the m-d diameter for M^2: "(i)n *Australopithecus* M^3 is almost invariably the longest upper molar" (p. 185). whereas in *Homo habilis* "either M^1 or M^2, but not M^3, is the longest of the cheek-teeth" (pp. 184-185). Another resemblance to *A. boisei* is in the very thick enamel of the molars and premolars (Beynon and Wood, 1986).

Although in some features it may resemble *Australopithecus*, particularly the robust species, KNM-ER 1805 lacks other distinctive features characteristic of these species, and in other features it resembles *Homo*. For example, although the dental enamel is very thick and within the range for *A. boisei* the prism pattern of the enamel is quite different from that of *A. boisei* and resembles early *Homo* (Beynon and Wood, 1986). The posterior teeth are also far below the observed range for *A. boisei* (Wood and Abbott, 1983) and in the root form of the P_3 KNM-ER 1805 shows the presumed primitive morphology for hominids rather than the highly derived root form seen in East African robust australopithecines (Wood et al., 1988). A canonical variates analysis based on measurements of the maxillary premolars and molars suggests that its closest affinities are with early *Homo* (Wood and Engelman, 1988).

Overall, there are enough similarities and resemblances to *Homo* in the relatively large cranial capacity, reduced postorbital constriction, and small mandible and cheek teeth, that KNM-ER 1805 is most often placed in this genus. Wolpoff (1980) and Howell (1978) have attributed it to *Homo erectus*, but it lacks many of the specialized features characteristic of this species (Wood, 1991) and with its cranial capacity intermediate between *Australopithecus* and *Homo erectus* and its retention of a number of primitive features, it is most often referred to early *Homo* or *Homo habilis*. It has also been suggested that the specimen's 'bizarre morphological configuration' might be the result of abnormal growth (White et al., 1981; c.f. Thompson, 1992).

KNM-ER 1813

In the first published description of this skull Leakey (1974) noted that it seemed to be quite different from the other hominid crania found at Koobi Fora: "The cranium, KNM-ER 1813, may prove to be quite distinct from the robust australopithecines and *Homo*, as represented by KNM-ER 1470. The dentition is 'hominine', yet the cranial capacity appears small. The cranium has some of the features seen in the gracile, small brained, hominid

Australopithecus africanus Dart, from Sterkfontein" (p. 655). In a provisional taxonomy of the Koobi Fora Plio-Pleistocene hominids Leakey (1974) proposed that the hominid fossils sampled three species: *A. boisei*, *Homo*, which incorporates specimens such as ER 1470 and 1590, and a third species, a gracile australopithecine which might be represented by KNM-ER 1813 and possibly OH 24 as well.

With its small cranial capacity, estimated by Holloway (1978) to be 509 cm^3, and a face that is large relative to its very small vault, KNM-ER 1813 has often been referred to *Australopithecus* rather than *Homo* or *Homo habilis*. Ferguson (1987b) has even gone so far as to claim that it represents the same species as AL 288-1. According to Ferguson (1987b) KNM-ER 1813 is far more primitive than *Homo habilis*, and he provides a long list of features in which it differs from KNM-ER 1470 and *Homo habilis* and resembles *A. afarensis*. Some of the features on this list (e.g. a relatively larger jaw) are not preserved on KNM-ER 1813 or KNM-ER 1470, nevertheless, Ferguson (1984) feels that the two belong to different species, with the former representing a male of the species *'Homo antiquus'*, a species which includes the gracile hominids from Hadar, such as AL 288-1(Ferguson, 1987a). On the other hand Leakey (1976a) who has been more than a bit ambiguous about KNM-ER 1813, noted that in some respects (which he did not specify) it resembles ER 407 and ER 732, which are generally considered to be female *A. boisei*, although in the same paper he noted that the relatively small dentition is suggestive of *Homo*.

The majority of workers who regard KNM-ER 1813 as an australopithecine, or see resemblances to *Australopithecus*, see similarities to the less primitive *A. africanus*. For example, Walker and Leakey (1978) pointed out that, with its small cranial capacity that is well within the australopithecine range, combined with a relatively large face and palate, KNM-ER 1813 strongly resembles *A. africanus*. Holloway (1978) explicitly identified it as *A. africanus*, although he qualified this with a question mark, whereas Olson (1978), based on a few morphological features of the nasal bones and cranial base, was even less equivocal

about the matter and attributed it to "*Homo* (i.e. *Australopithecus*) *africanus*". Overall, where it is preserved, the morphology of the nasal region seems to support such an attribution. KNM-ER 1813 lacks a prominent anterior nasal spine and the angle between the subnasal alveolar clivus and the floor of the nasal cavity is acute, but the inferior portions of the frontal process of the maxilla and the lateral walls of the nasal aperture are markedly everted. Because the nasal bones are damaged there is no way of determining whether they were flat or concave or whether or not there was an internasal angle. So, except for the eversion of the lateral nasal aperture and maxillary frontal process, KNM-ER 1813 retains the primitive australopithecine morphological pattern of a flat, non-projecting nasal region.

In spite of its resemblances to *Australopithecus* the majority opinion seems to be that KNM-ER 1813 belongs in the genus *Homo*, and there are a number of features which support such an attribution. According to Kimbel et al. (1984) KNM-ER 1813 differs from australopithecines and resembles *Homo* in having a shorter palate, a lower origin of the masseter muscle, a more tightly curved maxillary zygomatic process, a supraorbital sulcus, a relatively short nuchal plane and a relatively long occipital plane. To this list of resemblances Wood (1985) has added parietals that are relatively wider, reduced postorbital constriction, the depression of glabella, more orthognathic face, vertically oriented malar process, everted nasal margins, lateral orientation of the maxillary frontal process, shorter and wider cranial base, more coronally oriented petrous temporals, anterior position of porion and a foramen magnum that faces antero-inferiorly. The marked differences between KNM-ER 1813 and *Australopithecus* are even more apparent in the results of Bilsborough and Wood's (1988) multivariate analyses. In these analyses, which are based on facial measurements, KNM-ER 1813 does not fall close to the australopithecines, but rather occupies an intermediate position, between the australopithecines and *Homo erectus*. Metrically, the cranial base resembles that of *Homo erectus* (Dean and Wood, 1982), and Wood and

Engelman (1988) found that a canonical variates analysis based on the maxillary postcanine teeth also aligns KNM-ER 1813 with early East African *Homo* rather than robust or gracile australopithecines. Thus, in spite of its small cranial capacity, the morphology of the vault, face and postcanine dentition suggest that KNM-ER 1813 should be classified as early *Homo*.

Overall, the picture presented above is a confusing one. For each of the specimens discussed above there are some features that suggest affinities to *Australopithecus*, and the resemblances are strong enough that some workers have classified them as such. On the other hand, each of these crania also has features that align it with *Homo* and these specimens are often referred to this genus, sometimes individually and sometimes collectively. The resemblances to *Australopithecus* should not be surprising. If *Homo habilis* is a transitional species, bridging the gap between *Australopithecus* and *Homo erectus*, then it is to be expected that it in some respects it should be more primitive and australopithecine-like than later species of *Homo*.

The problem is that there does not appear to be any consistent pattern in the resemblances to *Australopithecus* and *Homo*. Thus, for example, KNM-ER 1470 resembles *Homo* in its large cranial capacity, expanded cranial vault, and in the morphology of the endocast and nasal region, but with its large, orthognathic face and anteriorly placed, deep and antero-inferiorly sloping malars it also resembles a robust australopithecine. On the other hand, the much smaller OH 24 is more similar to a gracile australopithecine: the face is small but large relative to the vault, which is also small, subnasal prognathism is pronounced and the face has a concave profile in lateral view, the nasal region retains the primitive morphological pattern and the malar slopes antero-inferiorly, but unlike KNM-ER 1470, it is narrow. The cranial capacity is small for *Homo* and large for *Australopithecus* but according to Tobias (1987, 1991) the morphology of the endocast is *Homo*-like. KNM-ER 1813 and 1805 also have their own idiosyncratic suites of australopithecine- and *Homo*-

like features, but there is no obvious pattern of resemblances that characterizes these crania as a group.

Homo habilis: How Many Species?

It is quite evident from the discussion above that OH 24 and KNM-ER 1470, 1805 and 1813 (and in fact all of the crania that have been attributed to *Homo habilis*) constitute a very heterogeneous group. So much so that it is not even clear that they all belong in the same genus. Nevertheless, they are all most commonly referred to *Homo*, and very often to the same species, *Homo habilis*. While it is acknowledged that there is a great deal of variation in this group, it is argued that the variation is not so great that it cannot be explained by sexual dimorphism, polytypism and perhaps evolutionary change within a single lineage. On the other hand, there are many paleoanthropologists who feel that the magnitude of variation is too great, and the pattern of variation too different, to allow for the assignment of all of these specimens to a single species and there have been a number of systematic attempts to prove this. These are discussed below, in chronological order.

Groves and Mazák, 1975

Groves and Mazák (1975) were the first to propose that there might be at least two contemporary species of early *Homo*. This idea was advanced in a paper in which the authors attempted to develop a taxonomy for all of the Plio-Pleistocene gracile hominids. Their analysis was based primarily on dental measurements, although they did give some consideration to the cranial and postcranial evidence as well. Decisions regarding whether or not the differences between hominid groups (defined by geography and chronology) are taxonomically significant were based on t tests and the coefficient of difference, which is a measure of the degree of overlap between two populations with respect to some continuous variable (Mayr et al., 1953).

The authors first considered the gracile hominids from Olduvai, comparing them with *A. africanus*. They argued that the differences in cranial capacity alone are sufficient to justify recognizing the two as different species, but they also noted that there are significant differences in the lower premolars: for the Olduvai hominids the premolars are much narrower. Although there is some variation within the Olduvai sample Groves and Mazák argued that they are not so great that they cannot be accounted for by sexual dimorphism and normal intra-populational variation. Thus, they concluded that the Olduvai gracile hominids are distinct from *A. africanus*, but only one species is represented. This is *Homo habilis*.

The gracile hominids from the upper levels at East Rudolf were argued to represent a different species than their contemporaries at Olduvai Gorge. This claim was based on the fact that all of the posterior teeth from East Rudolf are smaller than those from Olduvai, but the premolars lack the narrowing that is characteristic of *Homo habilis*. Additionally, the authors claimed that differences in the root morphology of the lower premolars from East Rudolf and Olduvai also point to separate species. In *A. africanus* the lower premolars typically have two separate roots, or the lower third premolars may sometimes have partially fused roots, whereas modern humans typically have single rooted lower premolars. According to Groves and Mazák most of the East Rudolf gracile hominids have single rooted premolars but they claimed (on the evidence of casts) that the Olduvai specimens most frequently have two roots and/or partially fused roots on the lower premolars. "Accordingly there is no doubt but that the middle and upper levels at Rudolf contain an undescribed hominid species" (p. 239). In fact OH 7, OH 13, OH 16 and OH 37 (an isolated mandible) all have single rooted P_4's and all have single rooted P_3's except for OH 7, which has two roots (Tobias, 1991; Wood, 1991, 1993). These are all of the mandibular premolars from Olduvai that have been attributed to *Homo habilis* by Tobias (1991) except for OH 6, a lower third premolar that shows no evidence of root formation.

This new species was given the name "*Homo ergaster*", from the Greek for 'workman', in reference to the stone tools found in the same levels as the hominid fossils. The type specimen for *Homo ergaster* is the mandible KNM-ER 992 and referred materials include the mandibles KNM-ER 730, 731, 820 and 1480, a number of teeth and KNM-ER 1805.

At that time it was believed that there was a substantial erosional event, representing approximately 700 kyr (Brock and Isaac, 1974), separating the strata below the KBS Tuff from those above the tuff, and the KBS Tuff itself had been dated to 2.6 Ma by Fitch and Miller (1970). Therefore the hominids from the Lower Member were believed to be much older than the *Homo* fossils from above the KBS Tuff and from Olduvai Gorge. According to Groves and Mazák these fossils represent two new species of gracile hominids. One of these possessed smaller teeth than *Homo habilis* or "*Homo ergaster*". This species, described as 'unequivocal Homo', is represented by the mandible KNM-ER 1501. The second unknown species is best represented by another mandible, KNM-ER 1482. This species had larger, especially broader teeth, which are equivalent in size to those of *A. africanus* but unlike *A. africanus*, this species shows a reduction in the premolar roots. The authors did not name either of these species, and they were unclear about which of them KNM-ER 1470 might belong to. Thus, according to Groves and Mazák there was not one, but at least four species of early *Homo*, some of which were contemporary with one another.

Wood (1985)

Wood (1985) concentrated only on the differences between the two most complete crania from East Turkana, KNM-ER 1470 and 1813. The main focus of this paper is on the issue of whether or not either, or both, of these hominids could be gracile australopithecines. Wood's systematic comparisons of these two crania with *A. africanus* led him to the conclusion that both are significantly different from gracile australopithecines and both are derived in the direction of *Homo* and should be included in that taxon. Wood

however, also compared the two crania with one another, in order to, "judge whether they are likely to belong to the same phenon grouping. Put simply, when examining the systematic relationships of KNM-ER 1470 and 1813, are we dealing with one taxon, or two?" (p. 211).

Wood begins by noting that, in spite of the obvious differences in size, the two are similar to one another in overall shape and in the proportions of the occipital. But he feels that the similarities in the shape of the vault are primitive retentions, whereas the similarities in the occipital "may be common to all taxa traditionally regarded as hominian and thus have no specificity beyond that of defining the *Homo* clade" (p. 212). The remainder of the discussion is given over to detailing the differences between KNM-ER 1470 and 1813. Wood notes that there are major differences in the shape of the face, particularly in the malar region; KNM-ER 1470 possesses a deep and forward angled malar whereas KNM-ER 1813 has a much smaller, excavated and backward sloping malar region. For Wood these differences seem to be more consistent with taxonomic variation rather than sexual dimorphism within a single species.

The most obvious difference between KNM-ER 1470 and 1813 is the disparity in size. To determine if this size difference is reasonable for two individuals who belong to the same species Wood compared the two using their estimated cranial capacities, which he cites as 770 cm^3 for KNM-ER 1470, and 510 cm^3 for KNM-ER 1813. He began by assuming that a coefficient of variation (CV) of 10 is, "a reasonable estimate for a hominid fossil taxon" (p. 212). This 'critical value' of 10 is based on CVs derived for extant and fossil samples, which are not identified. If the two crania sample a single species, the mean cranial capacity would be 640 cm^3 and, given a CV of 10, the standard deviation would be 64 cm^3. Consequently, Wood estimates that the 95% confidence interval for the mean would be 512 to 768 cm^3 (640 $\pm$ 128 cm^3). As Wood notes, "(t)he cranial capacity estimates of the two fossil crania thus lie almost exactly at these admittedly inexactly derived distribution ranges,

which should include approximately 95% of the population. The chance of one of the two crania being part of the population is thus 5%, with the chance of both crania being included correspondingly small (i.e. 2.5%)" (p. 212). KNM-ER 1590 probably had an even larger cranial capacity than KNM-ER 1470 (Holloway, 1978) and in Wood's view this makes it even less likely that specimens with cranial capacities of 510 and more than 770 cm^3 could be sampled from the same taxon. Wood concludes with the rather cautious statement, that "(t)hese statistical tests are simplistic, but nonetheless, when taken with the evidence of the facial differences, they suggest that KNM-ER 1470 and 1813 should not be uncritically regarded as belonging to the same taxon" (p. 212). Thus, according to Wood there are probably at least two species of early *Homo*, one represented by KNM-ER 1470 and the other represented by KNM-ER 1813. Wood did not make any suggestions concerning which species the two fossils should be referred to.

Stringer, 1986

Stringer (1986), like Wood, was interested in the question of whether or not the degree of variation in the collection of fossils attributed to *Homo habilis* is excessive for a single species, relying primarily on the CV to examine variation in cranial capacity and tooth size. Interestingly Stringer, unlike Groves and Mazák (1975), found little evidence for multiple species in the degree of dental variation, or in dental morphology. However, with respect to cranial capacity his results suggested to him that the degree of variation in *Homo habilis* is excessive for a single species. The CV of 12.4 for the *Homo habilis* sample (n=9) was larger than that of any of the fossil hominid (Ngandong and Neandertals) or extant hominoid (modern *Homo*, *Pan paniscus*, *P. troglodytes* and *Gorilla*) reference samples. The largest CV for a reference sample was 10.9 for *Gorilla* and only one other sample, modern *Homo sapiens*, had a CV greater than 10. On the basis of these values Stringer concluded that, "a coefficient of variation of about 10% is a reasonable figure for a hominoid species...." (p. 270). Since the CV for the *Homo habilis* was much larger than the critical value of 10 and

larger than any of the CVs for the reference groups, Stringer concluded that, "more than one taxon is being sampled" (p. 270). In sorting the different *Homo habilis* fossils for which endocranial volumes are known into different groups Stringer found that, "(w)hile two subsets can easily be created which each have the expected variation of 10% or less, this cannot be achieved while KNM-ER 1470 and 1813 are grouped together.... on this basis alone it is unlikely that these two fossils are conspecific unless a measure of special pleading is allowed" (p. 271).

Proceeding on the assumption that there is more than one species of early *Homo*, and that KNM-ER 1470 and 1813 represent different species, Stringer attempted to sort the mandibles and less complete crania attributed to *Homo habilis* into the two taxa, based on their resemblances to KNM-ER 1813 and 1470. On the basis of its flat upper and lower face OH 24 was placed in the same taxon as KNM-ER 1470 and based on its relatively large cranial capacity OH 7 was assigned to the same species, making the species represented by KNM-ER 1470 *Homo habilis*. The less complete larger crania, KNM-ER 1590 and 3732, as well as the mandible KNM-ER 1802 were also referred to *Homo habilis*. Stringer assigned the mandible KNM-ER 992 to the same species as KNM-ER 1813, making this species *Homo ergaster*, and into this taxon he also placed the smaller crania OH 13 and 16 and KNM-ER 1805. Thus, Stringer, agrees with Wood (1985) in finding evidence of multiple species of early *Homo* in the excessive degree of variation in cranial capacity. In particular the differences between the two most complete crania, KNM-ER 1470 and 1813, seem to be so great that it seems unlikely that they could be derived from the same species.

Lieberman, Pilbeam and Wood, 1988

Lieberman et al. (1988) focussed exclusively on the differences between KNM-ER 1470 and 1813, the two most complete, and most disparate early *Homo* crania. The authors attempted to take 'an explicitly probabilistic, quantitative perspective' in addressing the question of whether or not these two fossils could represent one species. This was done by

comparing the magnitude of variation between KNM-ER 1470 and 1813 with variation between randomly selected pairs of male and female gorillas. Gorillas were chosen as the comparative sample because they represent the extreme of sexual dimorphism for modern hominoids. In making these comparisons it was assumed that the differences between KNM-ER 1470 and 1813, if they are members of the same species, are due to sexual dimorphism: "KNM-ER 1470 is so much larger and shaped so differently from KNM-ER 1813 that it is reasonable to assume that KNM-ER 1470 would have to be a male and KNM-ER 1813 a female if both were to belong to the same species" (p.50).

In comparing the differences between KNM-ER 1470 and 1813 with the differences between male and female gorillas the authors were attempting to find the probability of sampling a male as large as KNM-ER 1470 and a female as small as KNM-ER 1813 from a population of hominoids as sexually dimorphic as gorillas. This was done by randomly picking one male and one female from the gorilla sample and then calculating the index of dimorphism (I_d; I_d = male value/female value) for cranial capacity and 26 linear measurements of the vault and face. Twenty such random male-female pairs were sampled. The distributions of I_ds obtained for the 20 pairs of gorillas were then compared with the corresponding I_ds for KNM-ER 1470/1813. The overall results seem to suggest that it is very unlikely that the two fossils could be derived from one species, even if that species were as sexually dimorphic as modern gorillas. Out of the 27 traits 8 had p-values of less than 0.05 (i.e. none of the I_d's for the gorillas were equal to or greater than the corresponding I_d for KNM-ER 1470/1813). Another 3 variables had p-values of 0.05 (i.e. the I_d for only one of the paired differences between male and female gorillas equalled or exceeded the corresponding I_d for KNM-ER 1470/1813).

On the basis of these results the authors concluded that both the magnitude and the pattern of the differences between KNM-ER 1470 and 1813 are inconsistent with their being derived from the same species. Differences in the pattern of variation are evident in the fact

that some of the variables for which KNM-ER 1470/1813 show excessive variation are variables which in modern hominoids tend not to be particularly sexually dimorphic. For example, the differences between KNM-ER 1470 and 1813 in measures of cranial width, such as maximum parietal breadth and minimum frontal breadth, were not matched in any of the 20 pairwise comparisons between male and female gorillas, but earlier work by Wood (1976a) has shown that cranial breadth measurements typically are not very sexually dimorphic. The metric comparisons also revealed differences in the proportions of facial width which seem to be unusual for males and females of the same species. For KNM-ER 1470 the mid-face is broader than the upper face, whereas KNM-ER 1813 shows the opposite pattern and the upper face is broader than the mid-face.

In addition to the metric differences Lieberman et al. identify several other differences between KNM-ER 1470 and 1813 that they feel are inconsistent with an explanation of sexual dimorphism. For example, they note that in addition to differences in the depth and orientation of the malar process previously identified by Wood (1985), there are unusual differences in the position of the malar root. In KNM-ER 1470 the maxillary root of the process is situated above P^4 and emerges closer to the alveolar process, whereas in KNM-ER 1813 the process originates higher on the maxilla and above M^1. According to Lieberman et al. this is opposite the pattern seen in extant hominoids where in males, which exhibit more subnasal prognathism, the root of the zygomatic is situated more posteriorly, between M^1 and M^2, and has a higher point of origin, and in the less prognathic females the malar emerges lower and more anteriorly on the maxilla, above M^1. There are also differences in the morphology of the supraorbital region which they identify as inconsistent with sexual dimorphism. The putative female, KNM-ER 1813, has larger and more prominent browridges than does KNM-ER 1470, the putative male, and KNM-ER 1813 also has a deep supraorbital sulcus, a feature which is completely absent in KNM-ER 1470.

On the basis of the metric and morphological differences between KNM-ER 1470 and 1813 Lieberman et al. came to the conclusion that:

> it is highly improbable that KNM-ER 1470 and ER 1813 could be from the same species unless either *Homo habilis* was substantially more sexually dimorphic than *Gorilla gorilla*, or sexual dimorphism in early *Homo* followed a pattern unlike that in extant higher primates..... In conclusion this study provides additional evidence that the taxonomy of the Late Pliocene-Early Pleistocene East African hominids needs to be revised and that at least one taxon needs to be created or recognized.... Separating what is now *Homo habilis* into two species would mean that two "gracile" hominids as well as *A. boisei* coexisted in eastern Africa about 2 My B.P. (p. 310).

Thus, Lieberman et al., like Wood (1985) and Stringer (1986), find evidence of multiple species of early *Homo* in the differences between KNM-ER 1470 and 1813, but the taxonomic differences are apparent in more than just the disparity in cranial capacity. They appear to be evident in both metric and morphological features, and suggest that the magnitude of variation is too great, and the pattern of differences too unusual, to be explained by sexual dimorphism alone.

Groves, 1989

Groves' assessment of taxonomic variation in early *Homo* was part of an ambitious attempt to revise the taxonomy of all fossil hominids. Like Wood (1985) and Stringer (1986) Groves relied on the CV as an indicator of taxonomic heterogeneity, comparing the CVs for samples of extant hominoids with those of fossil samples, in this case primarily for dental metrics. These comparisons were based on the proposition that within hominoid species CVs are nearly always less than 10, and "when higher values are obtained, one should become suspicious--of something or other" (p. 210). In addition, Groves attempted to use character analysis and cladistic methods to detect and identify species. Since Groves' early *Homo* dental sample had CVs greater than 10 for the upper canine dimensions (sample composition and sample sizes were not given) this sample was suspected of representing multiple species.

The early *Homo* fossils were divided into 'operational taxonomic units' (OTUs) on the basis of geography and the 'criterion of variability'. Three such OTUs were identified: 'Koobi Fora small *Homo*', represented by KNM-ER 1813 and KNM-ER 1805; *Homo habilis*, which consists of the gracile hominids from Olduvai; and the 'Koobi Fora Lower Member taxon', represented by fossils from below the KBS Tuff such as the crania KNM-ER 1470, 1590 and 3732 and the mandible KNM-ER 1802. Each of these three OTUs was given species status by Groves on the basis of patterns of shared apomorphic features. That is, within each of these groups there are, according to Groves, shared derived features not found in the other early *Homo* OTUs, indicating that they represent different species. The two species from Koobi Fora each possess two apomorphic features. The Lower Member taxon is characterized by the presence of a flat superior surface of the posterior zygoma and a lower canine area which is less than the P_4 crown area, whereas the small *Homo* taxon is distinguished by the presence of a flattened cranial vault and a broad P^3 whose mesiodistal (md) length is less than 75% of its buccolingual (bl) breadth. For *Homo habilis* there are eight apomorphic features, such as no supramastoid crest, basion located well in front of the bitympanic line, little lingual relief on the lower canines, no subsidiary cusp on P_3 and P_4 md diameter 'usually greater than 95% of bl breadth'.

In classifying the individual fossils Groves began with the mandible KNM-ER 992, the type specimen of "*Homo ergaster*" (Groves and Mazák, 1975). According to Groves it resembles the heavily damaged mandible of KNM-ER 1805 and probably belonged to a relatively small brained hominid, such as KNM-ER 1813. Thus, KNM-ER 1813 and 1805 were classified as *Homo ergaster*. The large-brained hominid from Koobi Fora represented by KNM-ER 1470 was given the name "*Homo rudolfensis*" (Alexeev, 1986), and the Olduvai gracile hominids retained the name *Homo habilis*.

Wood, 1993

Wood (1993) undoubtedly provides the most thorough and comprehensive assessment of variation in early East African *Homo*. Wood's early *Homo* sample consists of all of the cranial, mandibular and dental remains from East Africa that have been attributed to early *Homo* or *Homo habilis*, and includes fossils from Omo Shungura as well as the better known and more complete remains from Olduvai and Koobi Fora. Wood's analyses examine the magnitude and pattern of variation in a large number of dental, mandibular and cranial measurements as well as variation in the root and crown morphology and enamel thickness of the postcanine teeth. In addition, the early *Homo* sample is divided into two regional subsets representing Olduvai and the Omo Group deposits (Koobi Fora/Omo), and it is also broken up into 200 ka time bands. By looking at variation within and between these regional and temporal subsets Wood attempts to test various models that might account for the variation seen in early *Homo*. For example, the simplest model is that there is only a single, static species, *Homo habilis*. One alternative to this model is that there are two time-successive species. Other alternative models are that there were two synchronic, but allopatric species, or that there were two synchronic and sympatric species of early *Homo*, and so on.

Wood begins by comparing the magnitude of variation in the combined sample, within the two regional groups and within the temporal subsets, with variation in one species of extant hominoid, *Gorilla*, and two fossil hominid species, *A. boisei* and *H. erectus*. *Gorilla* was chosen as the modern comparative species because it is the most sexually dimorphic hominoid, and it is therefore a more appropriate reference group that less dimorphic species such as *Pan* or *Pongo*. When Levene's test for homogeneity of variances is used to determine if the differences in variation are significant only 5 variables (m-d diameter of the lower canine, the area of the lower third molar, the height of the palate, and the height and thickness of the mandibular corpus at M_1) show levels of variation which are significantly

greater than those of at least one of the comparative groups. Within some of the time bands and within some of the regional groups there also appears to be significantly more variation relative to the reference groups for some variables. Given the large number of comparisons being made however the presence of a few significant differences is not surprising, and overall the CV comparisons do not provide any convincing evidence for multiple species.

However, according to Wood there is evidence of multiple species in the pattern of variation seen within the early *Homo* sample, which does not seem to resemble the pattern of intraspecific variation within modern hominoids. In extant hominoids measurements of facial width are generally good sex discriminators, but there is little intraspecific variation in variables which measure the width of the cranial vault (Wood, Lu and Willoughby, 1991). According to Wood the fact that some variables for which the CVs are high in the early *Homo* sample are cranial breadth measurements seems to point to inter- rather than intraspecific variation. Furthermore, multivariate comparisons of the more complete crania (KNM-ER 1470, 1813 and OH 24) also suggest to Wood that the pattern of variation within early *Homo* is unusual for a hominoid species. Using canonical variates analysis Wood compares the relationships between the fossil crania with those of separate sex samples of extant large-bodied hominoids. When KNM-ER 1470 and OH 24 are compared with one another in this manner (Wood, 1993, Fig. 4, p. 504) the slope of the line joining KNM-ER 1470 and OH 24 is nearly orthogonal to the axes connecting the male and female centroids for *H. sapiens*, *Pan* and *Gorilla*, and it is strongly oblique to the line connecting the male and female orangutans as well. From this Wood concludes:

> The differences between the fossil axis and these comparative axes suggest that it is highly unlikely that the shape differences between the fossil crania resemble the pattern of difference between and male and female crania in the comparative sample. These findings provide strong evidence that sexual variation may be an insufficient explanation for the differences in facial shape between KNM-ER 1470 and crania such as OH 24. (p. 500)

The same pattern appears when KNM-ER 1470 is compared with KNM-ER 1813. The lines connecting the male and female centroids of *Pan*, modern *Homo* and *Gorilla* are oblique to the line connecting the fossils.

In addition to the metric comparisons variation in nonmetric traits is also examined to assess the likelihood of multiple species. If multiple species are represented then in "cladistic terms, there should be consistent differences in the expression of non-metric traits, or character states, between the taxa" (p. 490). According to Wood, there is an unusual pattern of variation in premolar root morphology which strongly suggests that there are multiple species of early *Homo*. The primitive hominoid condition, which is also seen in gracile australopithecines, is for the lower premolars to have two roots, whereas in modern humans these teeth typically have only one root. There is some intraspecific variation in the root morphology of the anterior premolar; in *Pan* single-rooted premolars occur at a relatively high frequency, and in modern humans Tomes root form, in which the apex of the root is bifurcate, occurs in low frequencies (Abbott, 1984, cited in Wood, 1993). Wood, like Groves and Mazák (1975), found that

> (T)he mandibular premolar root form of early *Homo* is remarkably variable, with its expression in both P_3s and P_4s varying from a single root, via Tomes' root form, to teeth with separate mesial and distal roots (Table 13). Two details are noteworthy. First, complex root forms are apparently confined to specimens from Koobi Fora, and second, within that group one specimen, KNM-ER 1802, has a premolar root size sequence that closely resembles that of the "robust" australopithecines (Wood et al., 1988: Fig. 7). Root form shows little intraspecific variation in the higher primates, but the P_3s of *Pan* do provide some evidence of sexual dimorphism. While the incidence of single-rooted P_3s is 20% (n=20) in males, nearly half, 46% (n= 11), of *Pan* females are single rooted. However, in the early *Homo* hypodigm it is the P_4 roots and not those of P_3 that display the excessive variability" (Wood, 1994, pp. 502-507).

Although he acknowledges that the case for taxonomic heterogeneity in early *Homo* is 'finely balanced', on the basis of these analyses Wood concludes that, "(t)he extent of the differences between the patterns of dental, gnathic, and facial variation within early *Homo* and those observed in the relevant comparators do suggest that the variability is more likely

to interspecific rather than intraspecific" (p. 508). These analyses also suggest that it is the Koobi Fora/Omo sub-sample that shows excessive variation. This is evident in the marked variation in the dimensions of the mandibular premolar crowns, in the multivariate differences between KNM-ER 1470 and KNM-ER 1813 and between the mandibles KNM-ER 1802 and KNM-ER 3734 and OH 13, and in the variation in premolar root form. All of these lines of evidence suggest to Wood that there are multiple taxa present in the Omo/Koobi Fora sample. The evidence for taxonomic heterogeneity in the Olduvai group is much weaker, but this could be due to the fact that the Olduvai sample is only half as large as the Koobi Fora/Omo sample.

In evaluating the hypothesis that there is a temporal component to the variation in the Koobi Fora/Omo regional sample Wood notes that KNM-ER 1470 and 1813 are approximately synchronous "and it is the approximate synchronicity of these two crania that provides the strongest evidence for two taxa being represented in that time band. Likewise, the same time band includes mandibular premolars with simple (KNM-ER 1501) and complex (KNM-ER 1802) root systems" (p. 511). On this evidence the hypothesis that temporal change is responsible for the variation in the Koobi Fora/Omo early *Homo* sample is ruled out. Wood favors the hypothesis that one species, *Homo habilis*, is present at Olduvai, and two species, *Homo habilis* and *Homo rudolfensis* are present and synchronous at Koobi Fora.

Wood also attempts to assign the cranial and mandibular fossils from Koobi Fora to these two species and to provide diagnoses for them. The diagnoses for *Homo habilis* and *Homo rudolfensis* are given in Table 2. Primarily on the basis of its phenetic resemblances to OH 24, particularly in the face, KNM-ER 1813 is identified as *Homo habilis*, making KNM-ER 1470 *Homo rudolfensis*. Wood describes KNM-ER 1805 as 'frustratingly enigmatic' but he feels that with respect to the shape of the face it resembles KNM-ER 1813 more closely than it does KNM-ER 1470. The less complete and more fragmentary crania KNM-ER 1590

TABLE 2. Cranial, mandibular and dental characteristics of Homo habilis *and* Homo rudolfensis *according to Wood (1993)*[b]

	Homo habilis	*Homo rudolfensis*
brain size	mean = 610 cm^3	mean = 751 cm^3
overall vault morphology	relatively large contribution of upper occipital scale to sagittal curve of vault	smaller contributiontion of upper occipital scale to sagittal curve of vault *
endocranial morphology	primitive sulcal pattern	frontal lobe asymmetry
cranial suture pattern	complex	simple
supraorbital morphology	incipient supraorbital torus	torus absent
parietal proportions	coronal chord longer than sagittal chord	sagittal chord equal to or greater than coronal chord
facial proportions	upper face broader than midface relatively prognathic	midface broader than upper face markedly orthognathic
nasal morphology	margins sharp and everted nasal sill present	less marginal eversion nasal sill absent
malar morphology	malar surface vertical or nearly vertical	malar surface inclined anteriorly
palate size	foreshortened	large
foramen magnum orientation	variable	inclined anteriorly
mandibular fossa depth	relatively deep	shallow
mandibular corpus morphology	rounded base moderate external relief	everted base marked external relief
mandibular teeth	postcanine tooth crowns buccolingually narrow M_3 reduced P_4 talonid reduced premolars have single roots	postcanine tooth crowns broad M_3 not reduced P_4 talonid relatively large P_3 with Tome's or two roots P_4 with two roots

and 3732 are placed in the same species as KNM-ER 1470 (*Homo rudolfensis*) and KNM-ER 3735 and 1478 are assigned to *Homo habilis*. The larger and more robust mandibles, KNM-ER 819, 1482, 1483, 1801 and 1802 are referred to *Homo rudolfensis* on the grounds that this is the larger species. In addition, it is argued that the large and orthognathic face of KNM-ER 1470 is an adaptation for heavy mastication, and the larger mandibles possess features which are also believed to be adaptations for heavy chewing, such as large cross-sectional areas, a well developed talonid in the premolars and complex premolar roots. The more gracile mandibles, KNM-ER 1501 and 1502, which have smaller canines and simpler premolar roots, are assigned to *Homo habilis*.

Rightmire, 1993

In his appraisal of cranial variation in early *Homo* Rightmire (1993), like many other workers who have addressed this problem, treats KNM-ER 1470 and 1813 as 'key individuals'. The less complete cranial remains are systematically compared with these two specimens in an effort to determine if one or more than one species is represented in this sample, and if multiple species are present, which fossils might belong to which species. To identify the similarities and differences between individual crania Rightmire relies on ratio diagrams, which show the proportional differences between fossils by comparing measurements relative to a particular specimen,

The ratio diagrams for the measurements of the vault seem to suggest that there are two morphological patterns present in the early *Homo* sample. The first pattern is represented by KNM-ER 1470, which has relatively long and broad parietals. It is also seen in KNM-ER 1590 and 3732. KNM-ER 1813 shows a different pattern, with parietals that are both sagittally short and transversely narrow. KNM-ER 1805 and OH 13, 16 and 24, resemble KNM-ER 1813 and also have parietals that are short and narrow.

The differences in the face appear to be more significant. The ratio diagrams show that KNM-ER 1813 and OH 24 are distinctly different from KNM-ER 1470, both have shorter

faces with lower cheek bones, smaller orbits and relatively low nasal apertures. KNM-ER 1813 and OH 24 also show a much greater degree of subnasal prognathism than the orthognathic KNM-ER 1470. There are differences between OH 24 and KNM-ER 1813 in the height of the cheek and the degree of projection at prosthion, but overall the two faces appear to be very similar to one another. Based on the similarities and differences evident in the ratio diagrams for the facial measurements Rightmire concludes that, "the two smaller *Homo* crania should be grouped together, while the larger Koobi Fora individual is unlikely to be a member of the same taxon" (p. 25).

According to Rightmire KNM-ER 1470 represents a relatively large-brained hominid, and KNM-ER 1813 and OH 24 represent a smaller brained form. In spite of its small brain size Rightmire attributes the species represented by KNM-ER 1813 and OH 24 to the genus *Homo* rather than *Australopithecus* on the grounds that it resembles the former in jaw morphology, tooth size and in the proportions of the face and vault. Since these two species of *Homo* were apparently synchronic the differences between them cannot be due to the effects of time and evolutionary change, nor does Rightmire feel that they can reasonably be explained by sexual dimorphism:

> A clearer sense that the variation among the two groups is not due to sex dimorphism emerges from the study of the faces. In the case of KNM-ER 1470, upper facial flattening as measured by the nasion angle is slightly less marked than in KNM-ER 1813 and substantially less than in OH 24. This is actually the reverse of the relationship expected, if the three crania are considered to belong to one taxon. Among the living hominoid primates males tend to have larger angles, reflecting greater flattening of the nasal root relative to the orbital margins....
>
> Much the same contradiction arises when patterns of lower facial projection are compared. Transverse facial flattening at subspinale.... is pronounced in KNM-ER 1470 while values for KNM-ER 1813 and OH 24 are lower by nearly 20°. This shows that there is more subnasal projection in the smaller skulls. However, in species of living hominoids, males have lower SSA values than females, and the latter should display the flatter lower faces.... Again, KNM-ER 1470 does not differ from the smaller specimens in the direction expected. Variation in facial proportions does not seem to be influenced primarily by sex. (p. 29)

Rightmire attempts to classify the less complete crania by comparing them with KNM-ER 1470 and 1813, the most complete representatives of the large- and smaller-brained forms of early *Homo*, respectively. Based on its large parietals and cranial capacity, which was probably in excess of 750 cm^3, Rightmire assigns KNM-ER 1590 to the same group as KNM-ER 1470. Although it is smaller than KNM-ER 1470 or 1590, KNM-ER 3732 is also assigned to this group, and Rightmire suggests that it may be a female, and KNM-ER 1470 and 1590 males. Of the Olduvai crania only OH 7, with its large parietals and a cranial capacity that was probably close to 700 cm^3 resembles KNM-ER 1470, and Rightmire attributes it to the large-brained morph, making this species *Homo habilis*.

For the smaller brained species of *Homo*, represented by KNM-ER 1813 and OH 24, Rightmire suggests that OH 13 closely resembles KNM-ER 1813 with respect to the size and morphology of the palate and the maxillary dentition, whereas OH 16 is only 'cautiously' assigned to the same taxon, since in some features it resembles the large brained hominids from Koobi Fora. Although it is intermediate in size between KNM-ER 1813 and 1470, KNM-ER 1805 is placed with the smaller-brained forms because of its resemblance to KNM-ER 1813 in the face, where it is preserved, and in the proportions of the parietal. The relatively large size of the vault and ectocranial crests suggest to Rightmire that it is a 'particularly robust' male of this species.

Kramer, Donnelly, Kidder, Ousley and Olah, 1995

The work of Kramer, Donnelly, Kidder, Ousley and Olah (1995) is the most recent attempt to resolve the question of taxonomic heterogeneity in early *Homo*. In this paper we take a novel approach to the problem by using randomization methods to compare the magnitude and pattern of craniometric variation in early *Homo* with variation in modern hominoids. The early *Homo* crania are systematically compared with reference samples of modern hominoids representing *Pan troglodytes*, *Pongo*, *Gorilla* and modern *Homo* using both univariate and multivariate measures of variation. The randomization methods, which

are described in detail in Chapter 6, are used to determine the significance of the measures of variation. Specifically, the randomization methods make it possible to determine the probability that the magnitude and/or pattern of variation in *H. habilis* can be matched by variation in living species of hominoids.

We, as in many of the studies discussed above, use the CV as the univariate measure of variation. For the univariate comparisons the *Homo habilis* sample consists of all East African crania that have been attributed to the species. Altogether seven individuals are represented. Variation in this sample is compared with variation in the reference samples for a total of 14 craniometric variables, for which sample sizes are between 2 and 7. Rather than using an arbitrary 'critical value', such as a CV of 10, to determine the significance of variation in early *Homo* randomization methods are used to compare the early *Homo* CVs with the CVs for the reference samples. For each variable this is done by randomly taking samples which are of the same size as the early *Homo* sample from the reference groups and building distributions of CVs with which the CVs for the fossils can be compared. The results of these comparisons suggest that relative to modern *Homo* and *Pan* the degree of variation in early *Homo* is excessive. For the early *Homo* sample 9 of the 14 variables have CVs which are significantly greater (i.e. $p<0.05$) than the corresponding CVs for the modern humans and *Pan*. However, when compared to the more dimorphic hominoids, *Pongo* and *Gorilla*, variation in *Homo habilis* does not appear to be as pronounced and the CVs for early *Homo* are insignificant for most variables. Interestingly however, there are two variables, external breadth of the palate (MAB) and minimum frontal breadth (MFB), which show significantly more variation in *Homo habilis* relative to any one of the four reference samples.

For the multivariate analyses we compare the most complete large *Homo habilis* cranium, KNM-ER 1470, with the two most complete small crania, OH 24 and KNM-ER 1813. For these comparisons the measure of variation is the multivariate distances between the

fossils, which are estimated from component scores derived from principal components analyses of the modern hominoids. The significance of the distances between KNM-ER 1470 and 1813, and between KNM-ER 1470 and OH 24 on the significant components is determined by comparing them with the distributions of equivalent pairwise distances between individuals in the reference samples. The results of the multivariate comparisons confirm the results of the univariate comparisons in demonstrating that, when compared to *Pan* and modern *Homo* variation in *Homo habilis* appears to be excessive. The distance between KNM-ER 1470 and 1813 on the first principal component is significantly greater than the corresponding pairwise distances in the modern human and chimpanzee samples. The distance between KNM-ER 1470 and OH 24 is also very large relative to these two species. However, these distances are not significant when compared to the distributions of pairwise distances for *Gorilla* and *Pongo*.

The univariate analyses compare the magnitude of variation in *Homo habilis* with the magnitude of variation in modern hominoids and in the multivariate comparisons the magnitude and pattern of variation are confounded with one another. It has been suggested that the pattern of variation in *Homo habilis* does not conform to the pattern seen in modern hominoids and is inconsistent with its being a single species. We attempted to evaluate this directly by comparing the profile of CVs for *Homo habilis* with the profiles of mean CVs for the reference samples. Differences in patterns of variation should be apparent in differences in the shapes of the CV profiles, that is, the profiles should not be parallel with one another. The CV profile for the modern hominoids do resemble one another in terms of shape, but the shape of the CV profile for *Homo habilis* differs from these profiles in several respects. The most obvious differences are seen in the large degree of variation in MAB and MFB in *Homo habilis*. In the reference samples these variables have small CVs, but in the *Homo habilis* sample they are among the most variable of measurements. Following a suggestion by Sokal and Braumann (1980) we use a rank order correlation to determine if the differenc-

es in the shapes of the CV profiles are significant, and these do seem to show that the pattern of variation in *Homo habilis* departs significantly from a pattern that is shared by modern hominoids.

Overall, the results of our analyses are somewhat ambiguous. The magnitude of variation seen in *Homo habilis* is excessive when compared to modern *Homo* and *Pan*, but it does not exceed the degree of variation seen in the more dimorphic pongids. Thus, for example, KNM-ER 1470 and 1813 could represent the same species if that species were as dimorphic as orangutans or gorillas, but it is not likely that they could be derived from a less dimorphic species. On the other hand, the pattern of variation in early *Homo* appears to be unique when compared to the modern hominoids. It is on the basis of the apparent differences in the pattern of variation that we draw the conclusion, albeit very tentatively, that there is more than one species of early *Homo*.

As a group, the analyses reviewed above would seem to provide strong support for the claim that there are multiple species of early *Homo*. A number of workers, looking at a variety of features and using different methods, have all come to the conclusion that *Homo habilis* actually represents more than one species. In addition, as discussed in the following section, variation in the postcranial fossils that have been attributed to early *Homo* also seems to point to the existence of more than one species. However, the case for multiple species is not as strong as it appears. Each of the studies above has its flaws and weaknesses, and proponents of the single species hypothesis have been quick to point them out and impose alternative interpretations on the data. These arguments for *Homo habilis* as a single species are reviewed below, after a brief discussion of the postcranial evidence for multiple species.

The Postcranial Evidence

Although all of the systematic analyses of variation in *Homo habilis* have focussed exclusively on the cranial and dental remains, the postcranial fossils that have been attributed to this species also seem to strongly hint at the possibility of multiple species. The first published descriptions of the *Homo habilis* postcrania from Olduvai (Day and Napier, 1964; Leakey et al., 1964; Napier 1962) emphasized the similarities between these fossils and modern *Homo*. But it now appears that there is a great deal of variation in the collection of postcranial fossils that have been attributed to *Homo habilis*. For some elements, such as the femur, the range of variation encompasses specimens which appear to be very primitive and australopithecine-like, and others which are much closer to the modern human morphology (Wood, 1974b). The different postcranial morphotypes were approximately synchronous and sympatric, and thus the more primitive forms do not simply represent earlier stages in the evolution of the modern human morphology.

In his description of the OH 7 hand Napier (1962) stressed those aspects in which the bones resemble modern humans. However, he also acknowledged that they, "cannot be closely matched with any known hominoid species living to-day" (p. 409) and identified a number of ways in which they differ from modern *Homo*. For example, in terms of robustness, shaft curvature and the development of the fibrotendinous markings the phalanges are unlike those of modern humans, and most closely resemble australopithecines and pongids (Napier, 1962; Susman and Creel, 1979; Susman and Stern, 1979, 1982). The proximal phalanges of KNM-ER 164, which are only slightly more recent than OH 7 (Feibel et al., 1989), are quite different from the Olduvai hand. Day (1978) describes them as being 'very modern in appearance' and "(s)imilar to modern human phalanges and different from those from Olduvai in that they are long and straight" (p. 326). In addition to the phalanges, KNM-ER 164 consists of a fragment of left parietal from near lambda which, according to Wood (1991), is "more likely to belong to *Homo* than

Australopithecus" (p. 107). Thus with respect to the morphology of the hand, two distinctive patterns are evident in early *Homo*, and the differences between them do not appear to be consistent with their belonging to the same species.

The OH 8 foot was identified as a paratype of *Homo habilis*, by Leakey, Tobias and Napier (1964) even though they believed that it was not associated with any cranial elements. However, Susman and Stern (1982) have suggested that the foot of OH 8 and the hand and cranial remains of OH 7 may all be from the same individual [see also Susman and Brain (1988)]. The OH 8 talus however, is very australopithecine-like (Day and Wood, 1968; Lewis, 1980; Wood 1974a; 1974b). A multivariate analysis showed that it is most similar to a robust australopithecine talus from Kromdraai and distinctly different from those of modern humans (Day and Wood, 1968). OH 8 and the Kromdraai talus do not even fall within the modern human range of variation. However, a similar multivariate analysis found that KNM-ER 813, a hominid talus from Koobi Fora which was approximately contemporary with OH 8, is quite different from OH 8 and very similar to modern human tali (Wood, 1974a). Thus, as Wood (1974a) has noted it would seem that:

> broadly contemporary with OH 8, is a talus that has a better claim to belong to a *Homo* foot. If the present taxonomic scheme is accepted an anomaly exists as the talar morphology of the two *Homo* specimens is very different. To postulate such wide variability of a key structure in one lineage is to introduce unacceptable complications into hominid phylogeny; a better solution would be to place these specimens in different taxa. When these new data are added to the fact that OH 8 is similar in some ways to the Kromdraai talus, it is a reasonable suggestion to attribute OH 8 to the genus *Australopithecus*. (Wood, 1974a:376)

The OH 8 foot, attributed to *Homo habilis* by Leakey et al. (1964), may not even belong to the genus *Homo*, or it may be the case that within the genus *Homo* there are two species, one of which retains a talar morphology that is more primitive and australopithecine-like, and the other of which is derived in the direction of modern *Homo*.

The diagnostic features of *Homo habilis* are in the teeth and skull. Since the association between OH 8 and the OH 7 cranial remains is tenuous, attribution of the former to *Homo*

habilis is questionable. In addition, the specimen only represents a small part of the postcranial skeleton. A more recent discovery from Olduvai, OH 62, provides much more information about the postcranial anatomy of *Homo habilis*. For this specimen there is no question about the association between cranial and postcranial remains. It was found in 1986 near the 'Zinj' site on the surface of Bed I sediments, and even though they were not discovered in situ it was possible to determine that the remains had eroded out of a level just below Tuff IC. Therefore it is slightly older than 1.75 Ma (Walter et al., 1991).

OH 62 is important because, although it is very fragmentary, it includes both cranial and postcranial elements. The palate and maxilla are the most informative parts of the skull that are preserved, and the most complete postcranial elements include a nearly complete humeral shaft, 2/3 of the radial shaft, most of an ulna, and the neck and proximal shaft of the femur. According to Johanson (1989), where it is preserved the face of OH 62, "most closely resembles specimens attributed to *Homo habilis* or *Homo sp.* (for example, OH 24, KNM-ER 1470, 1813, SK 847, and especially Stw 53). Specializations defining *Australopithecus africanus*, *A. robustus* and *A. boisei* are notably absent in the new Olduvai face" (p. 208). Primarily on the basis of its resemblance to Stw 53 Johanson et al. (1987) attributed it to *Homo habilis*.

The postcranial anatomy of OH 62 proved to be surprisingly primitive and australopithecine-like. Overall there is a strong resemblance to small *Australopithecus* individuals, particularly AL 288-1 (Johanson, 1989; Johanson et al., 1987). With respect to body size OH 62, which was an adult, is estimated to be as small or smaller than that of any known fossil hominid (Hartwig-Scherer and Martin, 1991; Johanson et al. 1987; McHenry, 1988). Interestingly, the reconstructed upper limb of OH 62 is longer than that of AL 288-1 but the femur (which was also reconstructed) is smaller. Thus, with an estimated humerofemoral index of 95 OH 62 falls outside the modern human range and is even more

like African apes in its limb proportions than is *A. afarensis* (Hartwig-Scherer and Martin, 1991; Korey, 1990).

In addition OH 62 resembles *Australopithecus* in several aspects of femoral morphology. The preserved portion of the OH 62 proximal femur possesses distinctive features which are diagnostic of *Australopithecus*. The characteristics that distinguish australopithecine femora from those of *Homo* are a small femoral head, a low neck angle, a long and antero-posteriorly compressed neck, and lack of an intertrochanteric line (Day 1969, 1978; McHenry and Corrucinni, 1976, 1978). For OH 62 the femoral head is missing, but according to Johanson et al. (1987) the estimated neck-shaft angle is approximately equal to that of AL 288-1 and the neck appears to have been long and flattened antero-posteriorly. The authors do not state whether or not an intertrochanteric line is present.

The unusual morphology of OH 62 is mirrored in KNM-ER 3735, a less complete *Homo habilis* specimen from Koobi Fora. The geological age of this fossil is between 1.88 and 1.9 Ma, making it a contemporary of KNM-ER 1470 and 1813. Although it is very incomplete and fragmentary, it includes both cranial and postcranial elements. The few cranial elements that are preserved suggest that the skull is that of a gracile hominid whose affinities are with the genus *Homo* (Wood, 1991). Tobias (1989) considers it to be *Homo habilis* and according to Leakey et al. (1989) the preserved parts of the skull are closer in size to KNM-ER 1813 than to KNM-ER 1470. The postcranial elements include the distal humerus, radius, ulna, femur and tibia, all of which are fragmentary and heavily worn (Leakey and Walker, 1985). A comparison of KNM-ER 3735 with AL 288-1 and OH 62 shows that these specimens all possess similar limb proportions, even though ER 3735 has larger absolute measurements for the fore- and hindlimbs (Leakey et al., 1989).

Contemporary with OH 62 and KNM-ER 3735 there are also postcranial specimens which lack australopithecine features and show stronger affinities with *Homo*. This is most evident in the sample of femora from the Upper Burgi Member of Koobi Fora. There are six

femora from Koobi Fora which were approximately synchronous with OH 62 but which lack the australopithecine features seen in the Olduvai specimen, such as the long antero-posteriorly flattened neck or the small neck/shaft angle. Not only do these femora lack the features typical of australopithecines, but they also strongly resemble the femora of *Homo erectus* (Kennedy 1983a, 1983b; Trinkaus, 1984). The resemblance is so strong that Kennedy (1983a, 1983b) claimed that the earliest specimen, KNM-ER 1481, is evidence that *Homo erectus* must have existed as early as 2 Ma.

For some paleoanthropologists the large differences in postcranial morphology are difficult to reconcile with the idea that there was only one species of gracile hominid in East Africa during the Plio-Pleistocene. On the basis of the postcranial evidence it has been suggested that there were actually two gracile hominid species, one of which retained a number of australopithecine-like features, such as small body size, ape-like limb proportions and australopithecine-like features in the femur, hand and foot. The smaller early *Homo* crania such as KNM-ER 1813 or OH 24, most likely represent the same species, which should probably be identified as *Homo habilis*. The second species, perhaps *Homo rudolfensis*, was larger and in some aspects of postcranial morphology this species was derived in the direction of later species of *Homo*. The differences between the two species in body size could account for much of the dental and cranial variation seen in early *Homo*.

The postcranial evidence may be suggestive of multiple species, but it does not provide an unequivocal answer to the question of taxonomic heterogeneity in early *Homo*, and it is possible to interpret the evidence differently. For example, Wolpoff (1996) points out that the size differences between the larger and smaller femora are not as great as the differences between femora from Hadar attributed to *A. afarensis*. However, it has recently been proposed that in the collection of femora attributed to *A. afarensis* the differences in size are so great that more than one species may be represented (Richmond and Jungers, 1995). More importantly though, as Wolpoff (1996) correctly points out, no postcranial remains

have been found associated with cranial remains attributed to *H. rudolfensis*. Thus, there is no way of knowing if the differences in body size can explain the apparent excessive variation in the skulls and teeth of early *Homo*.

Homo habilis as a Single Species

Collectively, the analyses by Groves (1989), Groves and Mazák (1975), Kramer et al. (1995), Lieberman, Pilbeam and Wood (1986), Rightmire (1993), Stringer (1986) and Wood (1985, 1993) seem to present a very strong case for the existence of multiple species of early *Homo*. Using a variety of methods, and based on a number of different metric and morphological traits, all of them have arrived at the same conclusion: there is probably more than one species of early *Homo*. However, each of these studies has its weak points, as some workers have been quick to point out, and it is possible to interpret the data in alternative ways. There are a number of workers [e.g. Howell (1978), Kimbel et al. (1984), Johanson (1989), Johanson et al. (1986), Miller (1991, 1994, 1995), Tobias (1991), White et al. (1981), Wolpoff (1996)] who maintain that there is only one species of early *Homo*, *Homo habilis*, and the variation in this species reflects nothing more than sexual dimorphism, polytypism and the effects of time and evolutionary change.

Each of the studies discussed in the previous sections has its own shortcomings and thus they do not, individually or collectively, prove unequivocally that there must have been more than one species of early *Homo*. Several of the claims for taxonomic heterogeneity in *Homo habilis* are based on the fact that for some variables the CV is greater than 10. On this basis it is claimed that the magnitude of variation exceeds the reasonable limits of intraspecific variation, and hence, more than one species must be present. Stringer (1986) and Wood (1985) make this claim with respect to endocranial volume, and Groves (1989) makes the same claim for upper canine dimensions. However, there is nothing magical about a CV of 10. Miller (1991) has shown that for endocranial volume CVs greater than 10 are often found in both large and small samples of modern hominoid species and a CV of

12.7 [for his *Homo habilis* sample Stringer (1986) obtained a CV of 12.4; Miller uses Sokal and Braumann's (1980) correction for bias in small samples, which gives a corrected value of 12.7] falls well within the range of single species CVs for hominoids. More importantly however, as Miller (1991) points out, the CV is an *estimate* of a population parameter and it has a standard error, which like any standard error is influenced by sample size. Thus, the large CV obtained by Stringer (1986) for endocranial volume in *Homo habilis* (n = 9) could reflect nothing more than random chance in the form of sampling error. The 95% confidence limits on this value provides some indication of how reliable it is as an estimate of variation in early *Homo*. The confidence limits are so broad (5.1 - 20.3) that they not only include the 'critical value' of 10, they also encompass the entire range of CVs for large samples in modern hominoids (Miller, 1991). Thus, there is no sound basis for claiming that the 'large' CV for cranial capacity in *Homo habilis* is proof or evidence of multiple species.

Lieberman et al. (1988) attempted to resolve the question of taxonomic heterogeneity in *Homo habilis* by taking 'an explicitly probabilistic, quantitative' approach and comparing the differences between two most disparate crania, KNM-ER 1470 and 1813 with the differences seen between randomly selected male-female pairs of gorillas. However, their sampling scheme involved a large number of variables (27) but too few comparisons (only 20 for each variable), to allow for an accurate assessment of how significant the differences between the fossils might be. The test procedure developed and used by Lieberman et al. is a randomization method using the index of dimorphism as the test statistic. As discussed in Chapter 6, randomization methods are particularly well suited for problems like that addressed by Lieberman and his colleagues. These methods require only a few simple assumptions about the data (Manly, 1991). One assumption however, is that if the null hypothesis is true then the variables have similar distributions in the groups being compared, and consequently the observed test statistic represents nothing more than sampling error. For each variable Lieberman et al. (1986) estimate their probabilities from the number of

comparisons between male-female gorillas which exceed the difference seen between KNM-ER 1470 and 1813. Thus, for example for those variables where only one of the male-female gorilla pairs had a value of l_d which exceeded the observed l_d between the fossils, they report a p-value of 0.05 (1/20), and for those variables where the l_d between the fossils was larger than all of the l_ds seen between pairs of males and female gorillas they give p-values of <0.05. However, in calculating the probabilities 1 should be added to the numerator and denominator, because if the null hypothesis is true the fossils represent a single species. That is, under the null hypothesis the comparison between the fossils represents one more comparison between individuals drawn from a single species and so 21 such comparisons were made by Lieberman et al.. Since the numerator is the number of comparisons that give a test statistic equal or greater than the observed test statistic 1 is added to the numerator to account for the observed l_d . Thus, for those variables where one male-female gorilla pair had an l_d greater than the observed l_d for the fossils, the correct p-value is 0.095 (2/21) and for those variables where none of the randomly chosen pairs of gorillas had an l_d greater than the l_d between the fossils the correct p-value is 0.048 (1/21). Any correction for multiple comparisons would result in a critical value smaller than the smallest possible p-value of 0.048.

In addition, Lieberman et al. (1988), and Rightmire (1993) as well, emphasize that the pattern of differences between KNM-ER 1470 and 1813 also seems to be inconsistent with an explanation of sexual dimorphism. For example, both Lieberman et al. and Rightmire note that in modern hominoids males are usually more prognathic than females, but KNM-ER 1813, the putative female, is more prognathic than KNM-ER 1470, the putative male. They argue that because the differences between KNM-ER 1470 and 1813 do not conform to the pattern of sexual dimorphism found in extant hominoids the fossils most likely represent different species. However, while it may be the case that within modern hominoid species males are typically more prognathic than females, it is not likely that all males are more

prognathic than all females, and it would probably be possible (although the probability may not be very large) to find male-female pairs where the female is more prognathic than the male. Comparisons such as these should be stated and tested in a probabilistic fashion, otherwise they are valid only if we are willing to make the dubious assumption that KNM-ER 1470 represents a typical or average male and KNM-ER 1813 an average female of *Homo habilis*.

Wood's multivariate comparisons between KNM-ER 1470 and 1813, and KNM-ER 1470 and OH 24, and males and females of modern hominoids suffer from essentially the same problem. In comparing the fossils with the male and female centroids for modern humans, *Pan*, *Pongo* and *Gorilla* Wood is comparing individual fossils with the centroids (means) for males and females within species. The comparisons between the fossils would only be meaningful if it is assumed that KNM-ER 1470 is an average male *Homo habilis*, and KNM-ER 1813 and OH 24 are average females. It is entirely possible that in Wood's multivariate comparisons a line or a number of lines connecting pairs of individual gorillas, for example, might show the same orientation or an even more oblique orientation to the line connecting the group centroids than the line connecting the fossils. The probabilistic method used by Kramer et al. (1995) is a more appropriate procedure for comparing the fossils, since the differences between the fossils are compared with the differences between individuals within the reference samples, but the results of our multivariate comparisons are ambiguous, and our interpretation of the results is critically dependent on what an acceptable degree of sexual dimorphism for *Homo habilis* should be: if *Homo habilis* were as sexually dimorphic as modern humans or *Pan* then it is unlikely that KNM-ER 1470 and 1813, or KNM-ER 1470 and OH 24, could both be derived from the same species, but if *Homo habilis* were as sexually dimorphic as *Pongo* or *Gorilla* then KNM-ER 1470 and the smaller crania could plausibly represent the same species.

Overall, the case for multiple species of early *Homo* is not nearly as strong as it appears, and many paleoanthropologists persist in arguing that *Homo habilis* is the only species of *Homo* preceding *Homo erectus*. Perhaps the greatest weakness of the multiple species argument is the simple fact that those who argue for this position cannot agree on which fossils represent which species, or even how many species of early *Homo* there might be. This is evident in Table 3, where the assessments of Stringer (1986), Groves (1989), Wood (1993), and Rightmire (1993) are summarized. Stringer (1986), Wood (1993) and Rightmire (1993), believe that there are only two species, one of which is *Homo habilis*. But according to Groves (1989) there are three, and Groves and Mazák (1975) identified four! Furthermore there is no agreement on how individual specimens should be classified. Thus for example, Rightmire (1993) believes that KNM-ER 1470 represents *Homo habilis* and OH 24 represents a second, unnamed species of *Homo*, but Wood (1993) classifies KNM-ER 1470 as *Homo rudolfensis* and OH 24 as *Homo habilis*, and Stringer (1986) believes that the two belong to the same species, *Homo habilis*.

Given the faults in the evidence and arguments for multiple species, and the inability to agree on the number of species and the taxonomy of individual specimens, many paleoanthropologists continue to maintain a strong skepticism when it comes to claims that *Homo habilis* represents multiple species, and there are a number of workers who argue that the variation seen in *Homo habilis* represents nothing more than sexual dimorphism, polytypism, normal intrapopulational variation, and perhaps the effects of time and evolutionary change (although the two most disparate crania, KNM-ER 1470 and 1813 are, within the resolution of the chronological framework, synchronous).

The two most prominent advocates of *Homo habilis* as a single species are Wolpoff and Tobias. Wolpoff's position is exemplified in his most recent defense of the single species hypothesis (Wolpoff, 1996) where he argues that those paleoanthropologists who recognize multiple species are emphasizing the differences between the specimens but overlooking the

TABLE 3. Classification of early Homo *fossils from Olduvai Gorge and Koobi Fora according to Stringer (1986), Groves (1989), Wood (1991), and Rightmire (1993).*

	crania	mandibles
Stringer, 1986		
Homo habilis	KNM-ER 1470, 1590, 3732 OH 7, 24	KNM-ER 1802
Homo ergaster (?)	KNM-ER 1813, 1805 OH 13, 16	KNM-ER 992
Groves, 1989		
Homo habilis	OH 7, 13, 16, 24 Stw 53	--------
Homo rudolfensis	KNM-ER 1470, 1590, 3732	KNM-ER 1802
Homo ergaster	KNM-ER 1813, 1805	KNM-ER 992
Wood, 1993		
Homo habilis	KNM-ER 1813, 1805, 1478, 3735, OH 7, 13, 16, 24, 52, 62	KNM-ER 1501, 1502 OH 37
Homo rudolfensis	KNM-ER 1470, 1590, 3732, 3891	KNM-ER 819, 1482, 1483, 1801, 1802
Rightmire, 1993		
Homo habilis	KNM-ER 1470, 1590, 3732 OH 7	--------
Homo sp.	KNM-ER 1813, 1805(?) OH 13, 16(?), 24,	--------

similarities and according to him the differences are not so extreme that we can confidently rule out intraspecific sexual dimorphism and polytypism as the cause.

> It could be assumed, and most often has been assumed, that specimens such as ER 1470 have larger brain sizes, and a robust dental and facial size and morphology that is quite similar to australopithecines, because the individuals are big. Limbs such as the ER 1472 and 1481 femora are often attributed to these larger crania, suggesting dramatic allometric differences. However, B. Wood questions whether the postcranial remains of habilines such as represented by OH 62 can be accommodated within the taxon represented by these large femoral remains from Koobi Fora? (p. 394)

Wolpoff claims that, "(t)he literal answer to Wood's question must surely be 'yes', this much difference *can be expected*" (p. 394, emphasis in the original) and to support his answer he notes that greater size differences can be found between large and small *A. afarensis* femora from Hadar and between modern human pygmy women and Nilohamatic men. Wolpoff then goes on to note that marked sexual dimorphism, which in some cases might have been equivalent to that seen in gorillas, is characteristic of many early hominid species and there is no reason to think that the habilines are an exception.

Wolpoff does not rule out the possibility of multiple species, but he does argue that

> the more conservative refutatory approach to this question fails to reveal sufficient evidence to reject the single species interpretation.... While the idea that there might have been two australopithecine-like early *Homo* species remains viable, a more likely explanation for this pattern of variation is that of numerous closely related populations with similarities and differences that reflect adaptation, genic exchange, and body size. Polytypism, so common in wide-ranging primates and ubiquitous through the course of subsequent human evolution, might be the best explanation for these relatively small habiline variations. (p. 395)

Of the three authors responsible for identifying and naming *Homo habilis* it was Tobias who took upon himself the task of defending the new species from its critics, and not surprisingly he has consistently and persistently maintained that *Homo habilis* is the only species of early *Homo*. Tobias's views on the question are summarized in his monograph on the *Homo habilis* cranial remains from Olduvai Gorge (Tobias, 1991). In this monograph Tobias examines a large number of morphological features and identifies the distribution of these characters in fossil hominids. Although the focus is on the fossils from Olduvai,

Tobias often includes specimens from Koobi Fora (particularly KNM-ER 1470 and 1813, but not KNM-ER 1805) in his *Homo habilis* sample, and it is clear from his treatment of these fossils that he believes that all of these specimens conform to the same general morphological pattern and represent the same species.

Although the monograph was published in 1991 it was apparently completed much earlier, and thus Tobias does not discuss the papers by Stringer (1986), Lieberman et al. (1986) or Groves (1989) in which it was argued that there is more variation in *Homo habilis* than can be comfortably accommodated in one species. Tobias does acknowledge the fact that there is a great deal of variation in his *Homo habilis* sample. However, he does not feel that this variation is so extreme that multiple species must be recognized, and his comparisons of CVs for endocranial volume in *Homo habilis* and extant hominoids show that for this character the degree of relative variation in *Homo habilis* falls within the range of variation for modern *Homo* and *Gorilla*, and only slightly above the range for *Pan troglodytes* and *Pongo*.

Many paleoanthropologists seem to prefer the single species interpretation not because they are strongly committed to it, but because they are unconvinced by the evidence for multiple species that has been presented to date. This position is exemplified in the following statement by Eldredge and Tattersall (1982), who acknowledge the possibility that KNM-ER 1470 and 1813 may not be conspecific, and that 1813 may be an australopithecine, but conclude their discussion of early *Homo* with the following statement:

> So what does the agglomeration of material commonly assigned to *Homo habilis* actually represent? We believe that at present it is impossible to be sure. We know that in the period following about 2 million years ago we find a good deal of variability in brain size among gracile hominids, together, apparently, with the general retention of a rather unspecialized structure of the skull. But whether we are dealing with one species, or two, or many, is difficult to tell..... For the present, then, we would choose to retain *Homo habilis* as a species of convenience, a term useful for identifying a particular suite of fossil material, but to which we would not attach an inordinate amount of biological significance. (p. 140).

CHAPTER 5

SAMPLE SELECTION AND DATA PROCUREMENT

Sample Selection

The early *Homo* samples

For both the dental and cranial comparisons, the early *Homo* sample is limited to specimens from East Africa. Cranial and dental remains from South Africa that may represent *Homo habilis* are not considered here because the taxonomy and affinities of these specimens is even less clear than the taxonomy and affinities of the east African fossils. The *Homo* fossils from Swartkrans, such as SK 847, may represent the same species as KNM-ER 3733, *Homo erectus*, but Grine et al. (1993) argue that it belongs to the same species as Stw 53 which they suggest could be *Homo habilis* or a new species of *Homo*. In addition, the chronology of the South African sites is so poorly resolved that the fossils could be contemporary with the East African specimens, or they could be younger by as much as 200 ka. Because of these uncertainties about their chronology, taxonomy and affinities the South African specimens that may belong to *Homo habilis* are not considered here.

The dental samples

The early *Homo* dental samples consists of teeth from three East African sites: East Turkana, Kenya; Olduvai Gorge, Tanzania; and Omo, Ethiopia. The number of anterior teeth attributed to early *Homo* is very small; for the incisors and canines sample sizes are between 2 and 5. These samples are simply too small to allow for any meaningful or accurate analysis of variation in these teeth, therefore this study is concerned only with variation in the posterior teeth, for which sample sizes are adequate. The samples comprise all

maxillary and mandibular premolars and molars identified by Wood (1993, Table 1, p. 486) as belonging to early *Homo* for which measurements are available. For these samples ***n*** is between 7 and 15. Sample sizes for the individual teeth are given in Table 4.

The crania

Of the cranial remains attributed to *Homo habilis* there are four specimens, KNM-ER 1470, KNM-ER 1805, KNM-ER 1813 and OH 24, which are complete enough that they can be compared using multivariate methods. These four fossils comprise the *Homo habilis* cranial sample used in this study. As discussed in Chapter 4 there is some question as to whether or not all of these fossils truly represent the single species *Homo habilis*, and it is not even certain that they all belong in the genus *Homo*. But all four have been attributed, either singly or collectively, to *Homo habilis* by a number of paleoanthropologists and currently there are many who feel that these four crania, along with a number of less complete specimens, represent only one species, *Homo habilis*, and that the variation in this group primarily reflects sexual dimorphism and perhaps polytypism, normal intrapopulational variation and the effects of time and evolutionary change.

KNM-ER 1470. This cranium was found in 1972 during the third season of the Koobi Fora Research Project. It was discovered when bone fragments identified as pieces of a hominid cranium were found washing down the slope of a gully. Subsequent screening of the area led to the recovery of more than 150 fragments. Although it was very fragmentary when found the reconstructed skull is relatively complete. It is preserved in two parts, the calvarium and the face. Detailed descriptions of the specimen and its preservation are provided by Day et al. (1976) and Wood (1991). The braincase is missing much of the occipital around the foramen magnum and little of the nuchal plane is preserved, but the occipital squama, the parietals, temporals and frontal are all present and fairly complete. Some fragments are missing, creating gaps in the vault, but the major landmarks can all be located with confidence. The face is complete along the midline from glabella to prosthion

TABLE 4. Sample sizes for early Homo *and* A. robustus *premolars and molars.*

mandibular teeth		maxillary teeth	
tooth	*n*	tooth	*n*
early *Homo*			
P_3	9	P^3	9
P_4	9	P^4	9
M_1	13	M^1	15
M_2	12	M^2	7
M_3	12	M^3	9
Australopithecus robustus			
P_3	17	P^3	17
P_4	17	P^4	21
M_1	28	M^1	22
M_2	23	M^2	21
M_3	21	M^3	22

and the nasal bones, the margins of the pyriform aperture and the medial walls of the orbit are preserved. The edges of the left orbit are largely intact, but the right orbit is missing much of the inferior margin. Parts of the left maxilla are missing, but the inferior orbital margin and the zygomatic process are both preserved so that malar height can be measured. The right maxilla is not as complete as the left. Except for the frontal processes the left and right zygomatic bones are missing. For the palate the alveolar process is present from the right M^1 to the left M^2 but the border of the alveolus is badly damaged and measures of palatal breadth must be estimated.

The facial portion can be articulated with the calvarium at nasion and there is also slight contact between the two on the left wall of the orbit, but the fit between them is not good enough to determine the exact orientation of the face relative to the vault. According to Wood (1991) small changes of the orientation of the face do not significantly change length measurements such as prosthion-inion cord. Nevertheless, measurements which involve both the face and vault and which might be affected by changes in the orientation of the face are not used here.

KNM-ER 1470 was found on the surface of the slope of a gully, but the matrix adhering to some of the fragments matched a layer of sand located near the top of the channel and about 35 m below the KBS tuff (Leakey, 1973a). On the basis of K-Ar and $^{40}Ar/^{39}Ar$ analyses the KBS tuff has been securely dated by McDougall (1985) to 1.88 ± 0.02 Ma. Since the stratum from which it is derived was deposited during the Olduvai Subchron (Hillhouse et al., 1986) KNM-ER 1470 must also be younger than 1.96 Ma, the most recent date for the top of the Olduvai (Hilgen, 1991; McDougall, 1992). According to Feibel et al. (1989) depositional rates at that time were very rapid (6 to 7 m per thousand years); therefore KNM-ER 1470 cannot be much older than the KBS tuff and they have assigned it a date of 1.88 to 1.9 Ma.

KNM-ER 1805. This partial cranium was found *in situ* in the lowest section of the KBS Member. The skull is incomplete and preserved in three main parts: the calvarium, the lower part of the face, and the corpus of the mandible. It is described by Day et al. (1976) and Wood (1991). The anterior portion of cranial vault is broken away just in front of the point where postorbital constriction is greatest. Thus, minimum frontal breadth can be measured but the length of the frontal cannot be determined. Except for the missing condylar and basilar parts of the occipital the remainder of the vault is largely complete and intact. The facial portion consists only of the distorted palate and lower face and the area around the nasal aperture. It cannot be articulated with the calvarium. Because there is so little of the face preserved, and much of what is preserved is deformed, the comparisons between KNM-ER 1805 and other hominids are based only on calvarial measurements.

KNM-ER 1805 was found above the KBS tuff in the very lowest part of the KBS member. Within this section of the KBS Member there are no unaltered tuffs that can be dated, but based on its position relative to marker horizons for which dates have been inferred Feibel et al. (1989) suggest a probable age of 1.85 Ma for KNM-ER 1805.

KNM-ER 1813. KNM-ER 1813 was found *in situ* in the Upper Burgi Member, below the KBS tuff. The specimen is described in detail by Day et al. (1976) and Wood (1991). When found it was fragmented and plastically deformed by matrix which had filled and expanded cracks in the vault. This distortion has been corrected by cleaning and reassembling the vault. Overall, KNM-ER 1813 is quite complete. The largest missing area is the left side of the face, where the malar region is missing. The zygomatic arch is missing on both sides as well. The remainder of the face is complete and intact: the palate is complete and undistorted; the margins of the right orbit and pyriform aperture are well preserved; and the right zygomatic is also present. The calvarium is relatively complete, the most significant gaps are in the cranial base where some of the area around the foramen magnum, all of the ethmoid, most of the sphenoid, and the right tympanic plate are missing. In addition,

some small fragments of the vault are missing, but overall KNM-ER 1813 is complete enough that all of the major dimensions of the face and vault can be measured or estimated with confidence.

KNM-ER 1813, like KNM-ER 1470, is derived from a layer that lies below the KBS tuff and within the Olduvai Subchron, and like KNM-ER 1470 it dates to the brief time interval between 1.88 and 1.9 Ma (Feibel et al., 1989).

OH 24. When this specimen was discovered in 1968 most of it was embedded in a limestone concretion. Additional fragments of the skull and teeth were recovered when the site was excavated and sieved. The cranium was very badly crushed and deformed but the reconstruction is relatively complete, although the vault is still somewhat distorted. Lists and descriptions of the preserved parts of OH 24 are given by Leakey et al. (1971), Clarke (1991) and Tobias (1991).

Much of the face is present and except for the zygomatic arches portions that are missing on one side are preserved on the other. The face is complete and intact along the midline from glabella to prosthion. Much of the right side of the face is also present; only the zygomatic process of the temporal and part of the maxillary alveolar process are missing on this side. The left side of the face is not as complete; much of the orbit is missing, with only small parts of the roof and medial wall present. The zygomatic and the zygomatic process of the maxilla are also missing on the left.

The vault is less complete than the face. The supraorbital torus is relatively complete and the frontal is nearly continuous along the midline from glabella to bregma. The frontal is complete enough behind the supraorbital torus to allow for a reliable estimation of minimum frontal breadth. The parietals are also intact along the midline but on both sides the lateral walls are completely missing. Thus, some dimensions of the parietals, such as maximum parietal breadth or the length of the parietals from sphenion to asterion, cannot be measured or estimated. The occipital squama is intact in the region of lambda and on the right side it

is preserved as far as asterion and the posterior border of the temporal. Only the medial portions of the left temporal are present but the right temporal is nearly complete.

In spite of the careful work of Clarke the reconstructed vault of OH 24 is still somewhat distorted (Clarke, 1991). Among other things the frontal is plastically deformed and flattened behind the supraorbital sulcus, which makes the entire sagittal profile of the vault along the frontal and parietals lower than it should be (see for example Tobias, 1991, Fig. 2, p. 57). Given this distortion the comparisons made here between OH 24 and other hominids which are based on measurements of the vault should be interpreted with caution.

OH 24 was found lying on the surface of an erosional gully but the calcareous matrix in which it was embedded is identical to limestone concretions found in a layer of tuffaceous clay in lower Bed I. This layer of clay overlies the basalt and is overlain in turn by tuff IB (Leakey et al., 1971). New dating results for lower Bed I deposits based on $^{40}Ar/^{39}Ar$ analyses of single mineral grains indicate that the basalt dates to 1.865 ± 0.007 Ma and tuff IB dates to 1.859 ± 0.004 Ma (Walter et al., 1991). Thus, temporally the Olduvai cranium falls between KNM-ER 1470 and KNM-ER 1813, which are somewhat older than OH 24, and KNM-ER 1805, which is slightly younger. Collectively OH 24, KNM-ER 1470, 1805 and 1813 represent a relatively brief period of time, between approximately 1.9 or 1.88 Ma and 1.85 Ma.

The reference samples

For fossil hominids the most appropriate extant reference species are the modern large-bodied hominoids. Of course, modern *Homo* is the species that is most closely related to fossil hominids and for this reason could be considered the most, or perhaps even the only appropriate reference group. For example, this is the approach taken by Grine et al. (1993) who used modern *Homo* as the only reference sample in their multivariate comparisons of Stw 53 and SK 847. In this study however, variation in the early *Homo* crania is compared with variation in every species of large-bodied hominoid except *Pan paniscus*. Among these

species there is a broad range of variation in terms of body size dimorphism which extends from modern *Homo*, the least sexually dimorphic species with males weighing 20 to 25% more than females, to *Gorilla*, where males weigh more than twice as much as females (Fleagle, 1988). Since the differences between the larger and smaller forms of early *Homo* are most commonly ascribed to sexual dimorphism by those who argue for a single species, comparisons with all of the large-bodied hominoids are made in order to determine how sexually dimorphic *Homo habilis* would have to be to accommodate all of the specimens that have been attributed to it. This also makes it possible to determine if this level of dimorphism is 'reasonable', that is, if it falls within the range of sexual dimorphism seen in modern hominoids rather than just one particular species of hominoid. There is no *a priori* reason for assuming that the degree of sexual dimorphism in early *Homo* is equivalent to sexual dimorphism in any one particular modern hominoid.

In addition to the comparisons with modern hominoids, variation in early *Homo* is also compared with variation in other species of fossil hominids. This is necessary because it is possible that fossil species as delimited by paleoanthropologists, encompass more variation than do extant hominoids. This may occur because fossil species are lineages with a time dimension and therefore exhibit more variation due to the effects of evolutionary change through time. It may also be the case that fossil species encompass more variation than extant species simply because paleoanthropologists are reluctant to recognize 'too many' species. In addition, if the results suggest that *Homo habilis* comprises more than one species, multivariate phenetic comparisons with other hominids may provide insights into the possible taxonomic affinities of these species.

The dental samples

For the comparisons of dental variation the reference samples consist of two modern hominoids, *Pan* and *Gorilla*, and one species of fossil hominid, *Australopithecus robustus*.

The modern hominoid dental samples: Pan *and* Gorilla. The modern hominoid samples consist of specimens from the Cleveland Museum of Natural History and the National Museum of Natural History (Washington D.C.). The chimpanzee dental sample consists of measurements from 34 maxillae and 31 mandibles for which the dentition is preserved well enough that a complete set of measurements (described below) could be taken. The maxillary sample comprises 22 females and 12 males and the mandibular sample consists of 18 females and 13 males. The gorilla dental sample comprises measurements taken from 37 maxillary dentitions (18 females and 19 males) and 36 mandibular dentitions (18 females and 18 males).

The fossil hominid dental sample: Australopithecus robustus. The fossil hominid comparative sample consists of robust australopithecine teeth from the South African sites of Swartkrans and Kromdraai. This sample represents a single species, *A. robustus*, which was chosen as a comparative group for several reasons. Most importantly the *A. robustus* dental sample is larger than that of any other Plio-Pleistocene hominid species and there is also general, but not universal, agreement that the robust australopithecines from Kromdraai and Swartkrans represent a single species. There are a few paleoanthropologists, most notably Grine (1985, 1988), who believe that there are two species of South African robust australopithecines: "*Paranthropus robustus*" (Kromdraai) and "*P.crassidens*" (Swartkrans). However, Grine's arguments for multiple species are not convincing. The two groups do differ with respect to a few minor characters of the deciduous dentition (Grine, 1985), but the differences do not appear to be great enough to warrant making a species distinction. Grine (1988) also cites differences in the size of the permanent cheek teeth as additional evidence for multiple species: "*P. robustus* values tend to be smaller than those of *P. crassidens* in permanent molar diameters....." (Grine, 1988, p. 234) whereas "*P. robustus* premolars tend to be large by comparison to the Swartkrans sample....." (p. 239). This last argument is based on simple comparisons of means and ranges, and given the small size of

the Kromdraai sample it is difficult to evaluate. Overall the differences do not appear to be unusually large and it has yet to be demonstrated that the two groups are *significantly* different from one another in any way. Consequently the great majority of paleoanthropologists recognize only one species: *A. robustus*. On this issue I side with the majority and use an *A. robustus* comparative sample that consists of teeth from both sites. For the *A. robustus* dental samples ***n*** is between 17 and 28. Sample sizes for the individual teeth are given in Table 4.

The crania

The modern hominoid cranial samples: Pan, Pongo, Gorilla *and modern* Homo. The modern hominoid comparative samples used in the multivariate analyses represent all of the extant species of large-bodied hominoids except *Pan paniscus*. The species represented are: modern *Homo sapiens*; *Pan troglodytes* (the common chimpanzee); *Pongo pygmaeus* (orang-utan); and *Gorilla gorilla*.

The pongid samples consist of crania from the collections of the Cleveland Museum of Natural History and the National Museum of Natural History (Washington, D.C.). Sample sizes are given in Table 5. All of the specimens are adults as determined by eruption of the full permanent dentition, including the third molar, and closure the basal synchondrosis. Gender attributions are from museum records. Within the comparative groups sample sizes for the face and vault differ because some specimens were damaged in a way that precluded obtaining a complete set of measurements (identified below) for the face or calvarium. For the chimpanzee comparative sample $n = 70$ for the vault (38 females and 32 males) and face (39 females and 31 males). This group consists primarily of specimens collected from Cameroon, but includes individuals from as far west as Guinea and as far east as Uganda. In addition, a few are of unknown geographic origin. The sample includes all three subspecies of *Pan troglodytes*: *P. t. verus*, *P. t. schweinfurthii* and *P. t. troglodytes*, with the latter making up the majority of the sample. For *Pongo* $n = 45$ for the vault (28 females and 17

TABLE 5. Sample sizes for the modern hominoids used in the multivariate distance comparisons.

species	females	males	total
Calvarial Measurements			
modern *Homo sapiens*	51	43	94
Pan troglodytes	38	32	70
Pongo pygmaeus	28	17	45
Gorilla gorilla	43	41	84
Facial Measurements			
modern *Homo sapiens*	47	39	86
Pan troglodytes	39	31	70
Pongo pygmaeus	37	27	64
Gorilla gorilla	42	42	84

males) and 64 for the face (37 females and 27 males). The sample includes both subspecies of orangutan, *P. p. pygmaeus* (from Borneo) and *P. p. abelii* (from Sumatra), as well as a few individuals of unknown geographic origin. The *Gorilla* sample is the largest pongid reference group, with $n = 84$ for both the vault (43 females, 41 males) and face (42 females and 42 males). This sample consists primarily of specimens from Cameroon, but also includes crania from Zaire and Rwanda and a few individuals whose geographic origin is unknown. All three subspecies of *Gorilla* are included in this sample. The majority of crania represent *G. g. gorilla* (the western lowland gorilla) and a much smaller number represent *G. g. graueri* (the eastern lowland gorilla) and *G. g. beringei* (the mountain gorilla).

All of the pongid reference groups include more than one subspecies and recent genetic studies of variation in mitochondrial DNA (mtDNA) in each of these species have caused some geneticists to propose that perhaps there are actually two species of orangutan, *P. pygmaeus* and *P. abelii*; two species of common chimpanzee, *P. troglodytes* (which would

include *P. t. schweinfurthii*) and *P. verus*; and two species of gorilla, *G. gorilla* and "*G. graueri-beringei*" (Morin et al., 1994; Ruvolo et al., 1994; Ryder and Chemnick, 1993). The marked intraspecific mtDNA differentiation seen in modern pongids may be indicative of multiple species of chimpanzees, orangutans and gorillas but without corroborating evidence in the form of distinct differences in nuclear DNA, morphology and behavior claims for multiple species should be treated as hypotheses to be tested rather than established facts. The available evidence demonstrates that although there is some morphological differentiation between subspecies in *Pan troglodytes*, *Pongo* and *Gorilla* these differences are not particularly marked and are not great enough to justify recognizing additional species (Albrecht and Miller, 1994; Courtenay et al., 1988; Groves, 1970; Shea and Coolidge, 1988; Shea et al., 1994).

The modern *Homo* reference sample consists of Native American crania from the collections of the University of Tennessee. This sample consists of skulls from a single location, the Larson site (South Dakota), a post-contact Arikara village and its associated cemetery. The site was occupied between 1679 and 1733 A. D. (Jantz and Owsley, 1984) and therefore, unlike the pongid samples, the modern *Homo* reference group represents, or is nearly equivalent to, a biological population. For the calvarium $n = 94$ (51 females and 43 males) and for the face $n = 86$ (47 females and 39 males). Attribution of gender is based on collection records. All of the specimens are adults as determined by closure of the basal synchondrosis and eruption of the permanent dentition.

The fossil hominid crania: Australopithecus boisei, A. africanus *and* Homo erectus. In addition to the comparisons with modern hominoids, the early *Homo* crania are also compared with other Plio-Pleistocene hominids. The number of hominid crania from this time period that can be included in these analyses is quite small. Excluding the four early *Homo* fossils described above, there are eight Plio-Pleistocene hominid specimens that are complete enough that they can be used here. These are listed in Table 6 along with their

TABLE 6. Plio-Pleistocene hominid fossils used in the multivariate analyses.

species	specimen	geological age (Ma)
early *Homo*	KNM-ER 1470	1.88 - 1.9
	KNM-ER 1805	1.85
	KNM-ER 1813	1.88 - 1.9
	OH 24	1.85 -1.86
Australopithecus africanus	Sts 5	ca. 2.4
	Sts 71	ca. 2.4
Australopithecus boisei	KNM-ER 406	1.65 - 1.7
	KNM-ER 407	1.85
	OH 5	1.78
Homo erectus	KNM-ER 3733	1.78 Ma
	KNM-ER 3883	1.5 - 1.65 Ma

[1]Geological ages are from Feibel et al. (1989) for the East Turkana crania, Walter et al. (1991) for the Olduvai Gorge fossils and Vrba (1982) and Schwarcz et al. (1994) for the South African fossils.

geological ages. Not all of these fossils are complete enough that they could be used in all analyses. Altogether these eight specimens most likely represent three different species: *A. africanus* (Sts 5 and Sts 71); *A. boisei* (KNM-ER 406, 407 and 732 and OH 5); and *Homo erectus* (ER 3733 and 3883). These fossils are derived from a time period between approximately 2.4 Ma and 1.5-1.65 Ma.

Sex attributions for these crania are more or less conjectural. Sts 5 and Sts 71 are both derived from Sterkfontein Member 4. Broom et al. (1950) considered both to be females, but it has also been suggested that the latter is female and the former male (Kimbel et al., 1984; Wolpoff, 1980) or that both are males (Rak, 1985). It has also been claimed that Sts 5 and Sts 71 represent different species (Clarke, 1988; Kimbel and White, 1988). Of the three *A. boisei* crania KNM-ER 406 and OH 5 are generally considered to be males whereas KNM-ER 732 is considered to be a female (e.g. Kimbel and Rak, 1993; Walker and Leakey, 1978; Wolpoff, 1980; Wood, 1991) but it has been suggested that two different species are represented (Groves, 1989). If these crania are conspecific the sex attributions are fairly sound. The differences between OH 5 and KNM-ER 406 on the one hand, and KNM ER 407 and 732 on the other, are in the size of the face and to a lesser degree the vault, in the presence and absence of ectocranial crests and in the degree of pneumatization of the cranial base. These differences consistently suggest that the former are males and the latter a female. Overall KNM-ER 3733 and 3883 are very similar to one another (Rightmire, 1990; Wood, 1991) and they are universally recognized as belonging to the same species, although what species that might be is the subject of some debate. Generally KNM-ER 3733 and 3883 are either classified as *Homo erectus* or as "*Homo ergaster*". For these two crania gender is uncertain. Wolpoff (1980) feels that KNM-ER 3883, with its more massive browridges, nuchal torus and mastoid processes is a male, and the more gracile KNM-ER 3733 a female. However, the differences between the two are not so great that they must be due to sexual dimorphism and they could be of the same sex.

Data Procurement

Dental measurements

For the early *Homo* dental sample the data are taken from Wood (1991, reference tables 21-24 and 26-29). The data for the *A. robustus* reference sample are primarily from Wood (1991) but these data are supplemented with dental measurements taken from Grine and Daegling (1993) and Grine and Strait (1994). Wood provides both buccolingual (b-l) and mesiodistal (m-d) crown diameters, with the latter measurements corrected for the effects of interproximal wear. These measurements are taken from occlusal photographs of the teeth, a method which makes it possible to reconstruct the original mesial and distal edges of the teeth and thus allows for reliable estimation of the unworn m-d crown diameters. As described below, the crown diameters for the modern reference samples, *Pan* and *Gorilla*, were collected for this study using calipers, a method which does not allow for accurate estimation of the original m-d length of worn teeth. Therefore, although it might prove to be very informative to look at variation in both the b-l and m-d dimensions of the posterior teeth, only b-l measurements are used here because of the problems created by interproximal wear.

For the fossil hominid teeth measurements are from whichever side is present. When equivalent teeth from both sides are present the diameter from the left tooth is used. Within an individual the crown diameters for antimeric teeth are strongly correlated with one another and including measurements for both the left and right teeth, when both are preserved, would have the effect of increasing n and decreasing the variance. Estimated in this way, with antimeres treated as though they are independent observations, the variance, or measures of variation derived from it, will not provide an accurate measure of the degree of variation among individuals.

For the modern reference species measurements of the buccolingual diameters of the maxillary and mandibular premolars and molars were made following Swindler (1976) and

Wood (1991). The buccolingual crown diameter is defined as the maximum crown diameter, at whatever height it occurs, along an axis perpendicular to the mesiodistal axis of the tooth with the mesiodistal axis defined as a line extending from the most mesial to the most distal point of the tooth. These measurements were taken with digital sliding calipers and recorded to the nearest tenth of a millimeter. When teeth from both sides were present measurements were taken from the left side unless the tooth on the right side was better preserved. Specimens were measured only if a complete set of maxillary and/or mandibular measurements could be taken.

Cranial measurements

Selection of the craniometric variables used in the multivariate analyses is based on several criteria: (1) the measurements for the fossils had to be available in the literature; (2) the measurements had to be clearly defined and replicable for all of the hominoid reference samples; and (3) the measurements were chosen to provide as complete coverage of the vault and face as possible, within the limits set by the first two criteria. Altogether 25 measurements satisfy these criteria. These are identified in Table 7 and more detailed descriptions are given in the Appendix. Collectively these measure the length and breadth of the frontal and parietals and the upper scale of the occipital, the height and width of the upper and lower face, the length and breadth of the nasal aperture, the length and breadth of the orbits, the width of the palate and the depth of the malar region.

The cranial measurements for early *Homo* and the other fossil hominids are all taken from a single source, Wood's monograph on the Koobi Fora cranial remains (Wood,1991, Reference Tables 1-13, pp. 313-332). Measurements for all but one of the specimens used here were taken by Wood on the original fossils, and thus the measurements are homologous from fossil to fossil. The only exception is OH 5; the craniometrics given by Wood for this specimen are from Tobias (1967). For bilateral measurements the measurements are

TABLE 7. Cranial measurements used in the multivariate distance comparisons.

Measurement	Variable
Calvarial Measurements	
cranial length (glabella-opisthocranion)	GOL
frontal chord (glabella-bregma chord)	GBC
frontal arc (glabella-bregma arc)	GBA
minimum frontal breadth	MFB
parietal chord (bregma-lambda chord)	PAC
parietal arc (bregma-lambda arc)	PAA
parietal coronal breadth (bregma-sphenion)	BSC
parietal temporal length (sphenion-asterion)	SPC
biasterionic breadth (asterion-asterion)	ASB
parietal lambdoid length (lambda-asterion)	LAC
maximum parietal breadth	XPB
biporionic breadth (porion-porion)	POB
Facial Measurements	
bijugal breadth (jugale-jugale)	JUB
superior facial breadth (frontomalare temporale-frontomalare temporale)	FMB
biorbital breadth (ektoconchion-ektoconchion)	EKB
orbital breadth (ektoconchion-maxillofrontale)	OBB
orbital height	OBH
interobital breadth (maxillofrontale-maxillofrontale)	IOB
nasal breadth	NLB
nasal height (nasospinale-nasion)	NLH
superior facial height (nasion-prosthion)	NPH
minimum malar height	MMH
maxillo-alveolar breadth (ektomolare-ektomolare)	MAB
palate breadth (endomolare-endomolare)	PLB
intercanine distance	CCB

from whichever side is better preserved and when both sides are present and equally well preserved measurements are from the right side.

For the modern hominoid reference groups measurements were collected for this study on the samples identified above. Great care was taken to insure that these are equivalent to Wood's measurements and for those that are landmark-based, that the same landmarks are used and that these landmarks are defined in the same way. When both sides were present bilateral measurements are from the right side, unless the left side was better preserved or landmarks on the left were more easily located. For some of the hominoids, particularly the male orangutans and gorillas, some landmarks (e.g. bregma and lambda) fall on crests, in which case Wood's convention of measuring from the plane of the surrounding vault was used.

CHAPTER 6

STATISTICAL METHODS

Univariate Methods

The magnitude of variation in the early *Homo* dental sample can only be evaluated by means of univariate methods. Even though the dental sample is much larger than the cranial or postcranial samples, there are relatively few specimens for which there are complete sets of posterior dental measurements and this precludes the use of multivariate measures of variation. Because the number of anterior teeth attributed to early *Homo* is too small to allow for any meaningful or accurate assessment of variation in the incisors and canines, this study is concerned only with variation in the size of the posterior teeth which is measured by the buccolingual dimensions of the mandibular and maxillary premolars and molars. As described in the previous chapter mesiodistal diameters are not used because of the problems created by interproximal wear.

Univariate measures of variation

The likelihood that multiple species are represented in a collection of fossils is most often evaluated by comparing the magnitude of variation in the fossils with that found in samples of closely related extant species. For continuous features these contrasts are almost always based on some univariate measure (or measures) of variation. There are many tests for homogeneity of variances, but these are rarely used and the variance itself is almost never used as a measure of variation. The most widely used measure is the coefficient of variation (CV), which is simply the standard deviation expressed as a percentage of the mean [CV = (standard deviation/mean) · 100]. Range based statistics, such as the range expressed as a percentage of the mean [R%; R% = ((maximum-minimum)/mean) · 100], or the maximum/minimum index (MI; MI = maximum/minimum) are also sometimes used to quantify relative variation. Martin and Andrews (1984, 1993) have claimed that the range-

based statistics have several advantages over the CV, and they suggest that the CV, R% and MI should all be used when comparing variation in fossils with variation in living species. Among other things it is argued that the range-based statistics are extremely conservative because they cannot overestimate variation, they can only underestimate it. Therefore the range-based statistics cannot lead to an incorrect rejection of the null hypothesis of a single species when it is in fact true. This would be a type I error. The CV however, may overestimate or underestimate variation, and reliance on the CV may result in type I or type II errors. A type II error would occur if the null hypothesis of a single species is not rejected when it is, in fact, false. Because the range-based statistics are unlikely to result in type II errors excessively large values of R% or MI are generally regarded as very strong evidence that more than one species is present in a sample (Cope, 1993; Martin and Andrews, 1984, 1993).

However, R% and MI are so conservative that they will often fail to detect multiple species in a mixed species sample. This problem is particularly serious when samples are small. Cope (1993) has shown that for mixed-species samples of closely related extant primates R% and MI will almost never be large enough to reject the null hypothesis of one species when n is less than 20. This is because the range is directly related to sample size; a large sample will have a larger range than will a smaller sample from the same population (Pearson, 1926). Therefore when samples are small the range provides a very biased estimate of variation, and the smaller the sample the more severe this bias will be. The range-based statistics are 'conservative' because they are such poor estimators of variation.

Unlike the range-based measures of variation the CV is an unbiased estimator of the parametric variance (Foote, 1993; Sokal and Rohlf, 1981). Through simulations Cope (1993) has demonstrated that, "the CV is simply a much more accurate estimate of the relative variation in the source population than any range-based statistic. This greater robusticity extends to sample sizes as small as five. In samples of $n=5$ or greater, it is

unlikely that range statistics will provide any information on relative variation that is not better represented by the CV" (p. 233). Using the CV may lead to more type I errors, but it will also result in many fewer type II errors. When testing hypotheses of multiple species there is no reason why one type of error is better or worse than the other, and the most reasonable approach is one which balances the chances of either type occurring.

How much variation is 'too much'?

Because the CV is simple to calculate and easy to understand it is the statistic used most often by paleoanthropologists for measuring variation and testing hypotheses of multiple species. If comparisons of the CVs of a fossil sample with those of a reference species indicate that there is more variation in the fossils than can be reasonably expected for a single species it is usually inferred that the fossils must represent more than one species. This would seem to be a relatively simple and straightforward proposition. However, determining how much variation is 'reasonable' or 'excessive' is greatly complicated by several factors. Often judgements about taxonomic heterogeneity are based simply on whether or not the CVs of the fossil sample exceed those of the reference species or some cutoff value derived from them. For example, Stringer (1986) suggested that for endocranial volume "a coefficient of variation of about 10% is a reasonable figure for a hominoid species" (p. 270). This conclusion was based on small comparative samples (the smallest *n* was 5, the largest 40) of modern hominoids and fossil hominids for which the CVs ranged between 8.6 and 10.9. Stringer's *Homo habilis* sample, with 9 individuals, had a CV of 12.4, "larger than that of any hominoid sample.... suggesting that more than one taxon is being sampled" (p. 271).

As has already been mentioned the CV is an unbiased estimator of population variation, even when samples are small. However, the standard error of the CV is a function of sample size; the smaller the sample the larger the standard error. The CV of a sample is an *estimate* of population variation. As sample size decreases the sampling distribution of the

CV encompasses an increasing range of possible values, and the estimate becomes less and less precise. Therefore, the CV may under- or overestimate population variation, and the smaller the sample the more likely it is that the CV is providing an inaccurate estimate of the parametric variance.

Fossil samples are nearly always small, and often they are very small, therefore the CVs of these samples may not be reliable estimates of population variation. It is possible to calculate the standard error and confidence limits for the CV (Sokal and Braumann, 1980) but they become very large when a sample is small. For example, the 95% confidence limit for Stringer's CV of 12.4 for *Homo habilis* is 5.1 to 20.3 (Miller, 1991). This confidence interval is so wide that it, "encompasses the entire range of CVs for large samples of extant hominoids" (Miller, 1991, p. 395).

The problem of comparing CVs is further complicated by the fact that there are no simple statistical tests for determining whether or not one CV is *significantly* greater than another. Tests for comparing two CVs for one character have been proposed by Sokal and Braumann (1980) and Cope and Lacy (1992), but they are only appropriate if the sampling distributions of the CVs are normal or nearly normal. They perform very poorly when the sampling distributions are asymmetric (Sokal and Braumann, 1980). Since the sampling distribution of the CV approximates a chi-square distribution (McKay, 1932; Warren, 1982) the distribution of CVs will not be normal when samples are small and tests based on a t distribution are inappropriate.

Recently two papers have appeared in which Monte Carlo methods were used to compare CVs and test hypotheses of taxonomic heterogeneity (Cope and Lacy, 1992; Kramer et al., 1995). Cope and Lacy (1992) developed a randomization procedure for finding critical values with which the CVs of a fossil sample can be compared. Their method of testing for multiple species in a fossil sample begins with the selection of one species from an appropriate set of reference species. This one species is the referent with

which the fossils are compared. The authors suggest that the best referent is either the sample with the largest ***n*** or the sample for which the CV is the median value of the CVs of all the reference species. They do not provide any rationale or justification for this choice. The mean and standard deviation of the chosen species is then used to simulate a large reference population from which a sampling distribution of CVs is generated. This is done by repeatedly taking, without replacement, samples of size ***n*** from the simulated reference sample, where ***n*** is the size of the fossil sample for the variable of interest. For each randomly drawn sample the CV is calculated, and by taking a large number of random samples a sampling distribution of CVs for samples of size ***n*** is created against which the fossil CV can be compared. Cope and Lacy use the 95th percentile of the sampling distribution as a critical value. If the fossil CV exceeds the critical value then the null hypothesis that only one species is represented in the fossil sample can be rejected.

Kramer et al. (1995) used a randomization approach somewhat similar to that of Cope and Lacy to compare craniometric variation in *Homo habilis* with variation in extant, large-bodied hominoids. However, rather than using a single reference species to find critical values for the CVs we directly compared the CVs of the *Homo habilis* sample with the CVs of large numbers of samples drawn randomly and with replacement from each of the reference samples. For each variable ***n*** for the random samples was equal to the ***n*** of the early *Homo* sample for that variable. The process of taking random samples and calculating their CVs was repeated 999 times, generating sampling distributions of CVs for each variable for each species. By simply counting the number of times that the CV of a random sample was equal to or greater than the CV for *Homo habilis* the authors estimated the probabilities of randomly obtaining a sample from a single hominoid species with the same ***n*** as the *Homo habilis* sample but which shows as much or more variation. Relative to all four species of hominoids the *Homo habilis* CVs for some variables had small p-values. For these

variables *Homo habilis* exceeds the reasonable limits of within species variation, which suggests that more than one species is represented.

A Randomization test for comparing variances

The problem of comparing variation in fossil samples with variation in living species is a problem for which the randomization and Monte Carlo methods are particularly well-suited. The fossil samples are invariably small (sometimes they are very small) and often they are much smaller than the reference samples with which they are being compared. When samples are small the CV or other measures of variation will have large standard errors and sampling distributions that are far from normal. All of these problems make it exceedingly difficult to evaluate the significance of variation in groups of fossils with standard statistical tests whose use is based on specific, restrictive assumptions, such as symmetric sampling distributions or approximately equal sample sizes.

The Monte Carlo simulations used by Cope and Lacy (1992) and Kramer et al. (1995) require only one or two simple assumptions (Good, 1994) and were developed to specifically take into account the potential problems created by small fossil samples, unequal sample sizes and a test statistic that has a non-normal distribution. However, in both tests the CVs of the fossil samples are treated as though they are accurate estimates, known without error, of the variation in the populations which they represent. This is a rather questionable assumption because the fossil samples are almost invariably small. For example, in the case of Kramer et al. n for the fossils ranged from 2 to 6. Given these sample sizes there is a strong probability that the fossil CVs are inaccurate estimates of population variation. Nevertheless, in the Monte Carlo simulations the fossil CVs are fixed values with which the CVs of the randomly chosen reference samples are compared. The CV of the fossil sample is treated as though it is known without error. Because of this, the question being tested by these simulations is not, "Is variation in the population represented by these fossils significantly greater than variation in this extant species?" It is rather, "If the fossils represent a

single species which is characterized by a relative degree of variation similar to that of the reference species, what is the probability that a sample of this size randomly taken from that species would be as variable or more variable than this sample?" The two questions are similar, but not quite equivalent.

In an attempt to address the first question, I use a randomization test for comparing variances which is similar to the bootstrap test described by Good (1993). This test is used to determine if variation in the early *Homo* dental sample, measured by the buccolingual diameters of the mandibular and maxillary premolars and molars, is excessive when compared with two extant hominoids, *Pan* and *Gorilla*, and one species of fossil hominid, *A. robustus*. The dental measurements were first transformed to the natural log scale in order to remove any potential differences in variances due to differences in morphological size. Within each sample the variables are then centered on their means for reasons outlined below. These deviates about the sample means are the observations used to compare variation between samples.

The rationale which is the basis for randomization tests is quite simple and straightforward: "Many hypotheses of interest in science can be regarded as alternatives to null hypotheses of randomness. That is to say, the hypothesis under investigation suggests that there will be a tendency for a certain type of pattern to appear in data whereas the null hypothesis says that if this pattern is present then this is a purely chance effect of observations in a random order" (Manly, 1991, p. 1). The only assumption needed for the randomization test is that, if the null hypothesis is true, the observations for the two samples being compared are identically distributed and therefore have the same degree of relative variation (Good, 1993; Manly, 1991). If this is the case then any differences in the variances of the samples are simply due to sampling error rather than differences in the variances of the populations from which they are drawn. Consequently, under the null hypothesis, observa-

tions from the two groups are interchangeable and any one allocation of individual observations to the two samples is as likely as any other.

The test involves comparing the ratios of the variances of the fossil and reference samples with distributions of variance ratios found by random allocation. Because the fossil and reference groups have different means the test cannot be performed on the log-transformed variables; this would be a test about the variance and the mean, a location parameter. Therefore each sample is first centered on its mean and the randomization test is performed on the centered observations. The test itself consists of combining the centered observations from the two samples being compared and randomly reordering them. The first n observations in the reordered sequence are assigned to the 'fossil sample', where n is the size of the original fossil sample, and the remaining observations are allocated to the 'reference sample'. The test statistic is the log of the ratio s_f^2/s_r^2, where s_f^2 and s_r^2 are the variances of the randomized 'fossil' and 'reference' samples, respectively. The test was carried out using a program written in MATLAB.

The variance, rather than the CV is used as the measure of variation because the samples are centered on their respective means and CVs cannot be calculated. The log of the ratio is used as the test statistic for ease of interpretation. If the variance of the 'fossil' sample is greater than that of the 'reference' the ratio will be greater than one and its log will be positive; if the 'reference' sample has a larger variance the ratio will be less than one and its log will be negative.

For each comparison with a reference species the randomization procedure is repeated 999 times, giving a sampling distribution of 999 log variance ratios with which the actual ratio can be compared. By comparing the observed ratio of variances with the distribution of randomized ratios it is possible to estimate the probability that the fossils represent a sample drawn randomly from a species with the same degree of relative variation as the reference species. This estimated probability is equal to $(c+1)/(r+1)$, where c is the

number of times the log ratio of the randomized variances is equal to or greater than one and r is the number of randomizations; for all tests $r = 999$. The one is added to the numerator and denominator because if the null hypothesis is true then the fossil sample represents a single species and the observed ratio of variances is simply due to random chance in the form of sampling error (Manly, 1991). If the fossil sample is significantly more variable than the reference only a small number of the randomized variance ratios will be greater than the observed ratio and the p-value will be small. This would suggest that, relative to the reference, variation in the fossil sample is excessive and it may therefore comprise more than one species. If the degree of variation in the fossils is not significantly greater than that of the reference species a considerable number of the randomized ratios will be greater than the observed ratio, and the p-value derived from these counts will be relatively large. A very large p-value, e.g. 0.998, would indicate that the fossil sample is significantly less variable than the reference species.

Levene's test for relative variation

Levene's test for relative variation (Levene, 1960; Schultz, 1983) is also used to compare variation in the early *Homo* fossils with that of the three reference species. Although there are a number of tests for homogeneity of variances many of them are not robust, and most of the tests that are robust lack power (Conover et al., 1981; Keselman et al., 1979). In a comparison of 56 different tests for homogeneity of variances Conover et al. (1981) found that in terms of robustness and power Levene's test using the median (Brown and Forsythe, 1974; Levene, 1960) consistently performs well under a variety of conditions. It has the additional advantage of being simple to use and easy to understand. The original samples, designated as the X_i's, are transformed to new values, $Y_i = | X_i - Md_i |$ where Md_i is the median for the i^{th} sample. The means of the transformed variables are a measure of the variation within the samples and an analysis of variance or a t test can be used to test for their equality.

The samples can be centered on some other measure of centrality, such as the mean or trimmed mean but the test is most robust when the median is used (Conover et al, 1981; Schultz, 1985). Schultz (1983) has suggested that to test for differences in relative variation the deviates about the median can be standardized by dividing them by the median ($Y_i = | X_i - Md_i | / Md_i$), or by first transforming the variables to the natural log scale and then centering on the median ($Y_i = | \ln X_i - Md_i (\ln X_i) |$). These tests are referred to respectively as the median-ratio and the median-log tests. Schultz (1985) has found that the median-log test is slightly more powerful when the underlying distributions are positively skewed, whereas the median-ratio test is slightly more powerful when the distributions are symmetrical or negatively skewed. Rather than choose one test or the other Schultz (1985) proposed that, "it will probably often be easier to simply perform both tests and choose the most significant result (Gans, 1984)" (p. 456). Both tests are used to compare dental variation in *Homo habilis* with dental variation in *A. robustus*, *Pan* and *Gorilla* using programs written in MATLAB.

Multivariate Methods

It is almost always the case that univariate measures of variation, such as the CV, are used to examine variation in a suite of measurements rather than a single measurement. For example, the randomization test for comparing variances is used here to compare variation in early *Homo* with variation in *Pan*, *Gorilla* and *A. robustus* for 10 dental measurements. The multiple comparisons can make interpreting the results of such analyses quite complicated, particularly when the comparisons are not independent of one another because of correlations among traits. For example, if for one out of ten measurements the CV of the fossil sample is significantly greater than that of a reference CV, with $p<0.05$, is that evidence for multiple species? What if two CVs are significantly greater in the fossil sample, or three? How many measurements must show significantly greater variation in the fossils before we can confidently conclude that multiple species are represented? And how

can we take into account the possible correlations between traits? Of course, the multiple comparisons increase the likelihood of obtaining significant p-values by random chance and making type I errors. It is possible to minimize this risk by using some adjustment for multiple comparisons, such as the Bonferroni adjustment, but since some of the traits may be correlated the adjusted p-values may be overly conservative and in any case, the problem of interpretation remains.

In addition, univariate measures of variation, such as the CV or variance, can only be used to determine if the *magnitude* of variation of each individual measurement being considered exceeds the reasonable limits of intraspecific variation in the fossils. They cannot be used to directly determine if the *pattern* of variation, i.e. shape differences, within a sample of fossils is reasonable for a single species. It has frequently been claimed that in early *Homo* the magnitude of variation for some metric traits is excessive relative to modern hominoids (e.g. Kramer et al., 1995; Lieberman et al., 1988; Stringer, 1986; Wood, 1985), but it has also been argued that the pattern of variation in early *Homo* is inconsistent with its being a single species (Kramer et al., 1995; Lieberman et al., 1988; Rightmire, 1993; Wood, 1991, 1993). With respect to this question univariate measures are largely uninformative, although Kramer et al. (1995) show that the profile of CVs for early *Homo* is distinctly different from the CV profiles of modern hominoids, and we cite this as evidence of shape differences within the early *Homo* sample that most likely reflect the presence of more than one species.

The potential problems caused by multiple comparisons and correlations between measurements can be circumvented by using multivariate statistics. Multivariate statistics also make it possible to look at differences in the pattern of variation (i.e. shape differences) in addition to differences in the degree of variation in early *Homo*. A randomization procedure like that used by Kramer et al. (1995) can then be used to determine how the multivariate distances between the fossils compare to the multivariate distances between

individuals sampled from modern species of hominoids. If the fossils represent only one species then the multivariate distances between them should not be significantly greater than the distances between modern hominoids that belong to the same species.

This methodology has enormous potential for resolving issues of taxonomy and heterogeneity and it is only just beginning to be applied to paleoanthropological problems (e.g. Grine et al, 1993; Jungers and Richmond, 1995; Kramer et al., 1995; Kramer and Konigsberg, 1994; Lee 1995). It is the basic approach employed here to determine if the most complete early *Homo* crania can reasonably be accommodated within a single species. The largest specimen KNM-ER 1470, is systematically compared with each of the three smaller specimens, KNM-ER 1813, KNM-ER 1805 and OH 24, to ascertain if the differences between them, measured in terms of a multivariate distance, exceed the reasonable limits of intraspecific variation for large-bodied hominoids. The results of Kramer et al. (1995) suggest that in modern hominoids size differences due to sexual dimorphism are more pronounced in the face than in the vault. This means that differences in the vault may be more informative than differences in the face. Therefore, separate multivariate analyses are carried out for measurements of the face and measurements of the vault.

The magnitude of the multivariate distances is evaluated by using a randomization routine to compare the multivariate distances between the fossils with distributions of distances between individuals within the modern hominoid samples. The distances between the early *Homo* crania are also compared with the equivalent distances within and between other species of Plio-Pleistocene hominids. In addition, the multivariate distances are decomposed into 'shape only' and 'size only' components using Burnaby's growth invariant discriminant function (Burnaby, 1966). This makes it possible to determine if the multivariate differences between fossils are primarily due to differences in size, differences in shape, or differences in both size and shape.

If the randomization tests suggest that the early *Homo* crania represent more than one species then there is a second question to be answered, and that is determining which species the individual specimens might represent, or which species they show affinities to. This second problem is addressed by using randomization and multivariate statistics to compare these fossils with other Plio-Pleistocene hominids.

A Randomization test for comparing multivariate distances

The Mahalanobis distance (D^2) is the test statistic used to measure the multivariate distances between the largest early *Homo* cranium, KNM-ER 1470, and each of the smaller crania, KNM-ER 1813, KNM-ER 1805 and OH 24. To determine if the D^2 between two fossils is plausible for hominoids that are conspecific the distance between the fossils is compared with pairwise distances between individuals within each of the four reference species, *Pan*, *Pongo*, *Gorilla* and modern *Homo*, by means of randomization tests.

The randomization test used here is very similar to that used by Kramer et al. (1995). The tests are based on pairwise comparisons between KNM-ER 1470 and KNM-ER 1813, KNM-ER 1470 and KNM-ER 1805, and KNM-ER 1470 and OH 24. For KNM-ER 1470 and KNM-ER 1805 the multivariate distance is based on measurements of the vault only, whereas for KNM-ER 1470 and KNM-ER 1813 and KNM-ER 1470 and OH 24 separate comparisons are made based on distances estimated from cranial measurements and distances estimated from facial measurements. The cranial and facial variables used for these comparisons are given in Table 8. The randomization procedure begins with the estimation of the D^2 between two fossils. Measurements are first transformed to the natural log scale and for each hominoid reference sample the variance-covariance matrix is estimated for the variables shared by the two fossils being compared. These are combined to give the pooled within-group variance-covariance matrix (W) and W is used to find the Mahalanobis distance between the two fossils being compared, where $D^2 = (\underline{x}_1-\underline{x}_2)' W^{-1} (\underline{x}_1-\underline{x}_2)$; $\underline{x}_1$ is

TABLE 8. Variables used in the multivariate distance comparisons with modern hominoids.

variable	KNM-ER 1470 - KNM-ER 1813	KNM-ER 1470 - OH 24	KNM-ER 1470 - KNM-ER 1805
Calvarial Variables			
GOL	+	+	
GBC	+	+	
GBA	+	+	
MFB	+	+	+
PAC	+	+	+
PAA	+	+	+
BSC	+	+	+
SPC	+		+
ASB	+	+	+
LAC	+		+
XPB	+		+
POB	+	+	+
Facial Variables			
JUB	+		
FMB	+		
EKB	+	+	
OBB	+	+	
OBH	+	+	
IOB	+	+	
NLB	+	+	
NLH	+	+	
NPH	+	+	
MMH	+	+	
MAB	+	+	
PLB	+	+	
CCB	+	+	

the vector of measurements for the first individual and $\underline{x}_2$ is the vector of measurements for the second individual.

To estimate the probability that the fossils represent one species an exact randomization procedure is used to compare the observed D^2 between the fossils (D^2_{obs}) with D^2 values between individuals within the modern reference samples. For each reference sample a distribution of within-species distances is generated by calculating all possible pairwise Mahalanobis distances between individuals in that sample. These pairwise distances are estimated in the same way as the distance between the fossils and are based on W and the vector of differences between the two individuals being compared. If n is the size of a particular reference sample there are $(n(n-1))/2$ possible pairwise distances for that sample. Because the reference distributions consist of all possible pairwise distances, rather than a random sample of these distances, the randomization is an 'exact randomization'. The probability that the fossils could be derived from a single hominoid species which is similar in the degree and pattern of variation to the reference species with which they are being compared is estimated by counting the number of pairwise distances in the reference distribution that equal or exceed D^2_{obs}. This probability is simply equal to $(c+1)/(np+1)$, where c is the number of pairwise distances in the reference that are greater than or equal to D^2_{obs} and np is the total number of pairwise distances in the reference distribution. The one is added to the numerator and denominator because if the null hypothesis is true the fossils being compared are members of the same species and the distance between them reflects intraspecific differences.

The differences between KNM-ER 1470 and the smaller crania, in particular KNM-ER 1813, which is much smaller than KNM-ER 1470, are so great that it is often assumed that if they are members of the same species KNM-ER 1470 must be a male, and the smaller specimens females. For example, according to Lieberman et al. (1988, p. 505) sexual dimorphism is

> the most logical explanation for the differences between the *H. habilis* fossils if we accept the hypothesis that they belong to the same species. Of the two relatively complete and adult *H. habilis* fossils, KNM-ER 1470 is so much larger and shaped so differently from KNM-ER 1813 that it is reasonable to assume that KNM-ER 1470 would have to be a male and KNM-ER 1813 would have to be a female if both were to belong to the same species (Wood, 1985).

This assumption is tested here by counting how many of the pairwise distances equal or exceed D^2_{obs} in each of the reference distributions are between males and females, between males and males, and between females and females. If a disproportionate number of these distances are between males and females it would suggest that if the fossils being compared belong to the same species the differences between them are most likely due to sexual dimorphism.

Partitioning the influence of size and shape

Most studies that have attempted to resolve (one way or the other) the issue of taxonomic heterogeneity in early *Homo* have concentrated on the size differences between the crania rather than the differences in shape (e.g. Groves, 1989; Lieberman et al., 1988; Miller, 1991; Stringer, 1986; Wood, 1985). But there is some evidence that the pattern of variation in early *Homo* is also inconsistent with its being a single species (Kramer et al., 1995; Rightmire, 1993; Lieberman et al., 1988; Wood, 1991, 1993). This is particularly true if most of the significant differences between KNM-ER 1470 and the smaller specimens, particularly KNM-ER 1813, are due to sexual dimorphism. The shape differences between these specimens do not appear to conform to the pattern of shape differences that distinguish males and females in extant species of hominoids (Lieberman et al., 1988; Rightmire, 1993; Wood, 1991, 1993). In order to evaluate the pattern of variation separately from the magnitude of variation Burnaby's size-adjusted discriminant function is used to partition the Mahalanobis distances between the fossils, and the corresponding pairwise distances within the reference samples, into 'size' and 'shape' distances.

Jolicoeur (1963) proposed that the first principal component of the pooled within-group variance-covariance matrix of log-transformed variables represents a general allometric size factor. Following this suggestion Burnaby (1966) showed how the effects of this size axis can be removed from D^2 leaving a 'size-free' or 'shape-only' distance. The ensuing explanation of Burnaby's method follows that given by Kramer and Konigsberg (1994). If W is the pooled within-group variance-covariance matrix of the log-transformed variables of the reference samples, then the first eigenvector of W (g) represents the general factor of within-species variation in size whose influence is to be removed. The Cholesky factorization of W^{-1} gives R, and the product of R is Δ (a p x 1 matrix, where p is the number of variables). Then the product of $\Delta/\Delta' \Delta\, I^{-1}\Delta$ is M, a p x p matrix. Finally, if $d=\underline{x}_1-\underline{x}_2$ then the 'shape-only' component of D^2 (D^2_{SH}) is $d'Qd$ where $Q=I-M$ (I is a p x p identity matrix). The 'size-only' component of the Mahalanobis distance (D^2_{SZ}) is equal to $d'Md$. The Mahalanobis distance should equal $D^2_{SH} + D^2_{SZ}$.

Partitioning D^2 into its size and shape components makes it possible to directly determine if, relative to modern hominoids, there are significant size and/or shape differences between the early *Homo* crania and if those differences are consistent with the specimens representing only one species. This is accomplished by means of the same randomization procedure used to evaluate the significance of the Mahalanobis distances between the fossils. Using Burnaby's method the D^2 between two fossils is decomposed into D^2_{SH} and D^2_{SZ}. The significance of these distances is then evaluated by comparing them with distributions of all possible pairwise size and shape distances between individuals in each of the four reference species and counting the number of distances in those distributions that equal or exceed the size distances and shape distances between the fossils. In addition, the possibility that the size and shape differences between the fossils are attributable to sexual dimorphism is evaluated by counting how many of the shape distances and how many of the size distances in the reference distributions that are equal to or greater than the corresponding

distances between the fossils are between males and males, between females and females, and between males and females.

Comparisons with other Plio-Pleistocene hominids

In addition to the comparisons with modern hominoids the distances between the early *Homo* crania are also compared with equivalent distances between Plio-Pleistocene hominids attributed to other species. Three species and two genera are represented by these other hominids: *A. boisei*, *A. africanus*, and *Homo erectus*. The individual specimens used for these comparisons are identified in Table 6. The purpose of these comparisons is to assess how the distances between the early *Homo* fossils compare to distances between fossil hominids that are generally considered to be conspecific (e.g. KNM-ER 3733 and KNM-ER 3883, or KNM-ER 406 and KNM-ER 407) and also how they compare to distances between fossil hominids that are definitely *not* members of the same species (e.g. KNM-ER 3733 and Sts 5, or Sts 71 and ER 406). It is possible that species of fossil hominids encompass more variation than do extant hominoid species because of the effects of time and evolutionary change, either as a result of directional selection, or because the direction of selection varies through time and thus causes the mean of a trait to fluctuate. Even fossils which are contemporaneous in terms of the geological time scale may be separated by thousands or tens of thousand of years, during which a significant amount of evolutionary change may occur. For example, in terms of the geological time scale KNM-ER 1470 and KNM-ER 1813 are synchronic, both are dated to 1.88 - 1.9 myr (Feibel et al., 1989). But if, for example KNM-ER 1813 actually represents the earliest part of this range and KNM-ER 1470 falls at the end of this time period they could be separated by ~20 kyr and perhaps a 1000 generations or more. A significant amount of evolutionary change can accumulate in this amount of time (Petry, 1982; Kirkpatrick, 1982) and the differences between the two crania

could reflect some combination of normal population variation, sexual dimorphism, and temporal change.

It could be argued that even if the differences between KNM-ER 1470 and KNM-ER 1813 are largely due to temporal change within an unbranched lineage they should still be considered different species if the differences are great enough, and in fact, this is the position taken here. Nevertheless, the possibility remains that species of fossil hominids may encompass more variation than extant species because of the time dimension. For this reason the distances between the early *Homo* crania are contrasted with the distances between other Plio-Pleistocene hominids. In addition, if the comparisons with modern hominoids suggest that more than one species is represented in the early *Homo* sample the distances between these crania and the other Plio-Pleistocene hominids may provide some insight on their taxonomic affinities. As discussed in Chapter 4, there is some question as to whether or not some of the early *Homo* specimens really even belong in the genus *Homo*.

Because of the fragmentary and incomplete condition of the fossils the distances among them are necessarily based on a smaller number of variables than the distances between the early *Homo* crania. For the face and vault separately several analyses are carried out using different fossil samples and different subsets of measurements in order to allow for the inclusion of fossils that are not as complete but which might be informative, such as KNM-ER 407 which is generally considered to be a female *A. boisei* (Wood, 1993), or KNM-ER 1805 which is the most unusual and enigmatic of the early *Homo* crania. For each analysis all pairwise D^2 distances between individual Plio-Pleistocene hominids are estimated using the pooled within-group variance-covariance matrix of the modern reference samples. The Mahalanobis distances between the fossils are then partitioned into size and shape distances using Burnaby's method. In addition, distributions of comparable distances are generated for the four reference samples by finding all possible pairwise distances within them. The median, the upper 95th and 99th percentiles, and the maximum distances for these

distributions provide some standards with which the distances between the fossils can be compared.

Principal coordinates analysis

If the randomization tests suggest that the early *Homo* fossils represent more than one species then the distances between these fossils and the other Plio-Pleistocene hominids may provide some insight into what species or genera the early *Homo* specimens might belong to or show affinities with. However, the number of dimensions in these distance matrices is one less than the number of fossils being compared. Therefore the matrices themselves are difficult to interpret and do not provide a clear picture of how closely the fossils resemble one another.

To provide a clearer picture of the phenetic similarities and differences between the fossils the dimensionality of the distance matrices is reduced by means of principal coordinates analysis (PCO). This is a method of summarizing the information in a matrix of distances by finding the principal components of the matrix and then representing the distances in terms of axes of variation. As in principal components analysis the first axis is the axis of greatest variation, the second axis is orthogonal to the first and represents the second largest dimension of variation, and so on. The relationships between the fossils can then be visualized by plotting their positions on the principal axes that account for the majority of the variation in the distances. PCO begins with the replacement of the off-diagonal elements of a distance matrix, x_{jk}, with $x^*_{jk} = -\frac{1}{2}(x_{jk})^2$. This matrix is then double-centered by subtracting the mean of all elements of row i and the mean of all elements of column j from x^*_{jk} and then adding to it the grand mean of all elements of the matrix. The normalized eigenvectors of the double-centered matrix give the coordinates of the original elements of the matrix on the principal axes, and the eigenvalues represent the amount of total variation accounted for by the eigenvectors (Gower, 1966). For example, if X is the matrix of eigenvectors, where $X = X_1, X_2 \ldots X_n$ and n is the number of observations, then X_{11}

and X_{22} give the coordinates of the first observation on the first and second axes, respectively, in the derived space. PCO is used to reduce the dimensionality of the Mahalanobis, size and shape distances between the fossils using NTSYS-pc (Rohlf, 1993). Of course, for the matrices of size distances there should only be one dimension of variation and in the matrices of shape distances one dimension of variation is lost because the size dimension has been removed.

CHAPTER 7

UNIVARIATE RESULTS: DENTAL VARIATION IN EARLY *HOMO*

Variation in the mandibular dentition

The descriptive statistics and CVs for the b-l diameters of P_3 - M_3 for early *Homo* and the three reference species are given in Table 9. Simple comparisons of the CVs seem to suggest that in early *Homo* there is a great deal of variation in the size of the posterior mandibular teeth. For early *Homo* the CVs for P_3 - M_3 are all larger than the corresponding CVs for *Pan* and *A. robustus*, and when compared to *Gorilla* only M_3 appears to show less variation. The CVs for P_3, M_1 and M_2 are nearly equal in early *Homo* and *Gorilla* and the CV for P_4 is much larger in early *Homo* (13.01) than it is in *Gorilla* (7.54). The differences between early *Homo* and the reference groups in the degree of relative variation in P_3 - M_3 are represented more clearly in Figure 1. In this figure it can be seen that the early *Homo* mandibular molars and premolars seem to show a much greater degree of relative variation in the b-l dimension than those of *Pan* and *A. robustus*, and for the third premolar and the first and second molars the degree of variation is equivalent to that seen in *Gorilla*. The most obvious difference between early *Homo* and the reference species is in the large degree of variation in the b-l diameter of P_4 in early *Homo*. For this measurement the early *Homo* CV is much larger than those for any of the reference groups.

The results of the randomization test for equality of variances, presented in Table 10, demonstrate that most of the apparent differences between early *Homo* and the reference species in the degree of relative variation are not significant. If a ***p***-value of 0.05 is used as the significance level for the individual contrasts few of the differences between early *Homo* and any of the reference groups are significant. Since, the only outcome of interest is if the variance in the early *Homo* sample is larger than the variance of a reference group, all of the contrasts are one-sided and significant differences in the variances indicate that the variance in early *Homo* is greater than that of the reference group. For early *Homo* the variance in P_3

Table 9. Descriptive statistics and coefficients of variation for early Homo *and reference samples: Mandibular dentition.*

tooth	*n*	mean	s.d.	CV
early *Homo*				
P_3	9	10.07	1.28	12.71
P_4	9	10.87	1.41	13.01
M_1	13	12.52	0.92	7.33
M_2	12	13.47	1.10	8.17
M_3	12	13.21	1.01	7.66
A. robustus				
P_3	17	11.66	0.89	7.63
P_4	17	12.88	0.94	7.28
M_1	28	13.76	0.88	6.42
M_2	23	14.91	0.99	6.61
M_3	21	14.70	0.99	6.76
Pan				
P_3	31	8.49	1.01	11.88
P_4	31	8.50	0.54	6.36
M_1	31	9.64	0.48	5.02
M_2	31	10.38	0.56	5.40
M_3	31	9.85	0.62	6.29
Gorilla				
P_3	36	11.92	1.51	12.64
P_4	36	12.41	0.93	7.54
M_1	36	13.18	0.98	7.46
M_2	36	15.09	1.23	8.15
M_3	36	14.61	1.39	9.49

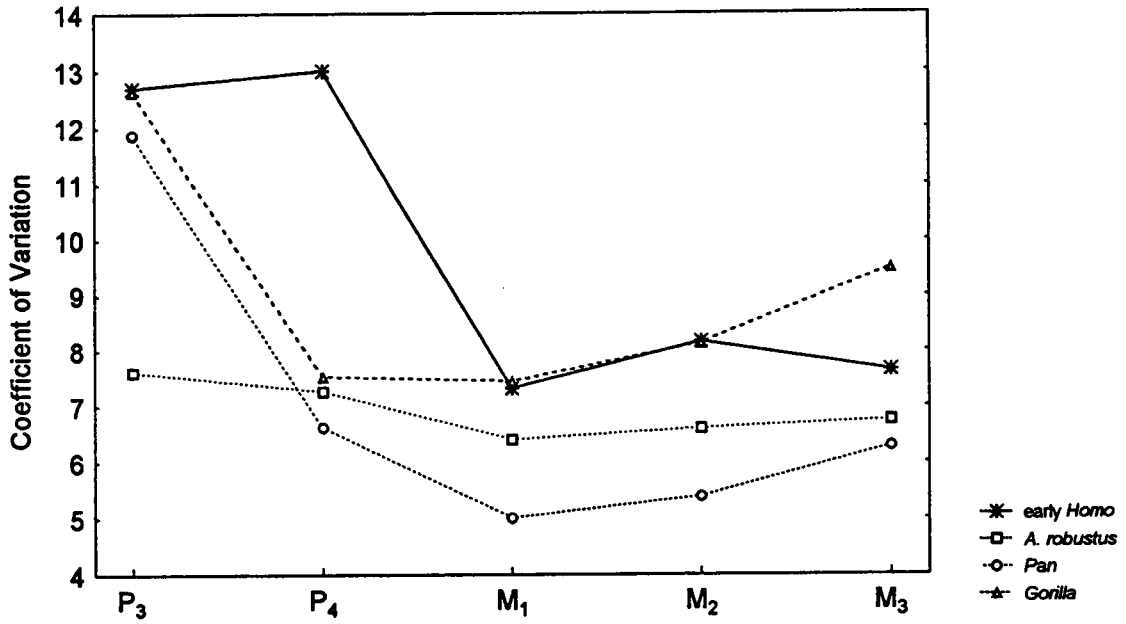


Figure 1. Coefficients of variation for the mandibular postcanine teeth of early Homo, A. robustus, Pan *and* Gorilla.

b-l is nearly significant when compared to *A. robustus* and this is also true for the contrast between *Pan* and early *Homo* for M_1 b-l ($p = 0.052$ for both contrasts) and for M_2 the difference between *Pan* and early *Homo* is significant ($p = 0.042$), but the only consistent significant difference between early *Homo* and the reference groups is in the degree of variation in P_4 b-l. For this measurement the variance in early *Homo* is significantly greater than the variance in any of the reference groups. For the contrast with *A. robustus* only 43 of the variance ratios of the randomly generated '*A. robustus*' and 'early *Homo*' samples equal or exceed the observed variance ratio ($p = 0.044$); for the contrast with *Gorilla* only 16 of the variance ratios obtained by random reallocation equal or exceed the observed ratio ($p = 0.017$); and for the contrast with *Pan* only 6 of the of randomized variance ratios are equal to or greater than the observed ratio ($p = 0.007$).

Table 10. Results[a] of the randomization test for comparing variances: Mandibular dentition.

s_f^2	reference	s_r^2	ln (s_f^2/s_r^2)	*c*	*p*
P_3 b-l					
0.0171	*A. robustus*	0.0063	0.9988	51	0.052
	Pan	0.0135	0.2360	296	0.297
	Gorilla	0.0157	0.0808	403	0.404
P_4 b-l					
0.0188	*A. robustus*	0.0052	1.2896	43	0.044
	Pan	0.0040	1.5451	6	0.007
	Gorilla	0.0059	1.1648	16	0.017
M_1 b-l					
0.0056	*A. robustus*	0.0043	0.2725	252	0.253
	Pan	0.0025	0.8002	51	0.052
	Gorilla	0.0057	-0.0133	481	0.482
M_2 b-l					
0.0067	*A. robustus*	0.0044	0.4156	171	0.172
	Pan	0.0030	0.8044	41	0.042
	Gorilla	0.0068	-0.0225	494	0.495
M_3 b-l					
0.0058	*A. robustus*	0.0045	0.2521	255	0.256
	Pan	0.0040	0. 3737	136	0.137
	Gorilla	0.0091	-0.4465	831	0.832

[a] s_f^2 = variance of log-transfomed measurements for early *Homo*; s_r^2 = variance of log-transfomed measurements for reference samples; ln (s_f^2/s_r^2) = log of the ratio of s_f^2 and s_r^2, values > 1 indicate that the variance is greater in early *Homo* and values < 1 indicate that the variance is greater in the reference species; *c* = number of randomized log variance ratios equal to or greater than 1.

However, if a Bonferroni adjustment is used to correct for the multiple contrasts being made in each comparison, several of the differences which are significant when the individual significance level is 0.05 are no longer so. With a family significance level of 0.05 for the comparisons on each variable the significance level for each contrast is 0.017 (3/0.05). For M_2 the variance in early *Homo* is no longer significantly greater than the variance in *Pan*, and the same is true for the contrast between early *Homo* and *A. robustus* for P_4. The only significant differences that remain are between early *Homo* and *Pan* and *Gorilla* for P_4 b-l.

The results of Levene's median ratio and median log tests for relative variation, presented in Tables 11 and 12, respectively, are somewhat similar to the results of the randomization test, although the median ratio and median log tests appear to be more conservative; the *p*-values are consistently larger than those obtained by the randomization tests. As is the case for the randomization test all of the probabilities are one-sided, and significant *p*-values for a contrast indicate that the variance of the early *Homo* sample is significantly greater than the variance of the reference sample with which its being compared. The results given in Tables 11 and 12 show that if a significance level of 0.05 is used for the individual contrasts the only significant difference between early *Homo* and the reference groups is for P_4 b-l. For this measurement the variance in early *Homo* is significantly greater than the variance in *A. robustus* ($p=0.024$ and 0.019 for the median ratio and median log tests, respectively), *Gorilla* ($p=0.019$ and 0.021) and *Pan* ($p=0.009$ and 0.007). However, when an adjustment is made for the multiple contrasts for each variable, making the individual significance level 0.017 rather than 0.05, only the difference between *Pan* and early *Homo* is significant.

Table 11. Results of Levene's median ratio test for relative variation: Mandibular dentition.

reference species	fossil mean - reference mean	*t*	*p*
P_3 b-l: $F_{3,89}$ = 1.53, p=0.212			
A. robustus	0.044	1.49	0.069
Pan	0.016	0.57	0.284
Gorilla	0.001	0.03	0.488
P_4 b-l: $F_{3,89}$ = 1.99, p=0.121			
A. robustus	0.037	2.00	0.024
Pan	0.040	2.40	0.009
Gorilla	0.035	2.09	0.019
M_1 b-l: $F_{3,104}$ = 1.29, p=0.280			
A. robustus	0.004	0.30	0.384
Pan	0.013	1.00	0.160
Gorilla	-0.006	-0.45	0.675
M_2 b-l: $F_{3,98}$ = 1.54, p=0.208			
A. robustus	0.011	0.73	0.233
Pan	0.019	1.26	0.105
Gorilla	-0.003	-0.20	0.578
M_3 b-l: $F_{3,98}$ = 2.44, p=0.069			
A. robustus	0.012	0.75	0.228
Pan	0.013	0.86	0.197
Gorilla	-0.013	-0.91	0.816

Table 12. Results of Levene's median log test for relative variation: Mandibular dentition.

reference species	fossil mean - reference mean	*t*	*p*
P_3 b-l: $F_{3,89} = 1.51$, $p=0.219$			
A. robustus	0.046	1.58	0.059
Pan	0.018	0.68	0.247
Gorilla	0.005	0.17	0.433
P_4 b-l: $F_{3,89} = 2.16$, $p=0.099$			
A. robustus	0.040	2.10	0.019
Pan	0.044	2.50	0.007
Gorilla	0.036	2.07	0.021
M_1 b-l: $F_{3,104} = 1.30$, $p=0.277$			
A. robustus	0.005	0.35	0.365
Pan	0.015	1.07	0.143
Gorilla	-0.005	-0.38	0.647
M_2 b-l: $F_{3,98} = 1.49$, $p=0.225$			
A. robustus	0.011	0.71	0.240
Pan	0.017	1.16	0.125
Gorilla	-0.004	-0.28	0.610
M_3 b-l: $F_{3,96} = 2.47$, $p=0.067$			
A. robustus	0.011	0.69	0.244
Pan	0.012	0.81	0.211
Gorilla	-0.014	-0.97	0.834

Variation in the maxillary dentition

The means, standard deviations and CVs for the maxillary posterior teeth of early *Homo* and the three reference groups are given in Table 13, and the CVs are plotted in Figure 2. For all of the b-l diameters the CVs for the early *Homo* sample exceed those of *A. robustus*, with the largest differences in the CVs for M^2 and M^3. The only marked differences between early *Homo* and the two modern hominoids are in the degree of variation for M^2 and M^3: the CVs for early *Homo* (10.06 for M^2 and 9.52 for M^3) are much larger than the equivalent CVs for *Pan* (6.28 for M^2 and 6.67 for M^3) or *Gorilla* (7.75 for M^2 and 7.94 for M^3). In addition, for P^3 the early *Homo* CV (7.05) is greater than the CV for *Gorilla* (6.14) and for M^1 the early *Homo* CV (5.82) is greater than the *Pan* CV (5.02), but these differences do not appear to be particularly large.

The results of the randomization test for equality of variances, given in Table 14, show that most of the differences between early *Homo* and the reference groups are not significant. If a significance level of $p = 0.05$ is used for the individual contrasts only four of the differences are statistically significant. None of the variances for early *Homo* are significantly greater than the corresponding variances in the *Gorilla* dental sample, but for M^2 and M^3 the degree of relative variation in early *Homo* is significantly greater than the relative variation seen in *Pan* ($p = 0.048$ for M^2 and 0.018 for M^3) and *A. robustus* ($p = 0.043$ for M^2 and 0.001 for M^3). If an adjustment is made for the multiple contrasts for each variable and a p-value of 0.017 is used as the significance level for the individual contrasts only the difference between early *Homo* and *A. robustus* for M^3 b-l is significant. For this contrast none of the variance ratios obtained by randomization are as large as the observed ratio. The difference between early *Homo* and *Pan* is nearly significant for the same variable.

Tables 15 and 16 present the results of the median ratio and median log tests for relative variation for the maxillary posterior teeth. If a significance level of 0.05 is used for each contrast only the differences between early *Homo* and *A. robustus* for M^2 are significant

Table 13. Descriptive statistics and coefficients of variation for early Homo *and reference samples: Maxillary dentition.*

tooth	*n*	mean	s.d.	CV
early *Homo*				
P^3	9	12.04	0.85	7.05
P^4	9	12.06	0.77	6.35
M^1	15	13.23	0.77	5.82
M^2	7	14.85	1.49	10.06
M^3	9	14.68	1.39	9.52
A. robustus				
P^3	17	14.06	0.70	4.95
P^4	21	15.23	0.81	5.34
M^1	22	14.84	0.65	4.40
M^2	21	15.95	0.84	5.25
M^3	22	16.93	0.65	3.82
Pan				
P^3	34	9.98	0.79	7.88
P^4	34	10.10	0.62	6.12
M^1	34	11.31	0.57	5.02
M^2	34	11.62	0.73	6.28
M^3	34	10.93	0.73	6.67
Gorilla				
P^3	37	15.35	0.94	6.14
P^4	37	14.98	0.95	6.35
M^1	37	15.22	1.04	6.85
M^2	37	16.35	1.27	7.75
M^3	37	15.28	1.21	7.94

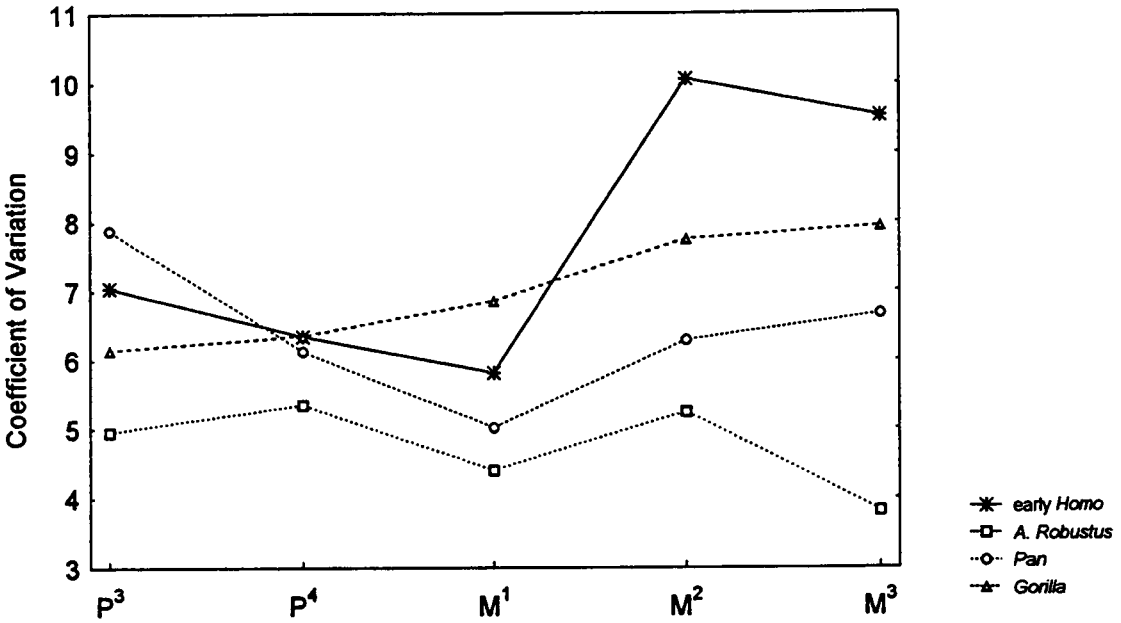


Figure 2. Coefficients of variation for the maxillary postcanine teeth of early Homo, A. robustus, Pan *and* Gorilla.

($p = 0.043$ for the median ratio test) and M^3 ($p = 0.003$ for both the median ratio and the median log test), but when an adjustment is made for multiple contrasts the only significant difference between early *Homo* and *A. robustus* in the degree of relative variation is for M^3 b-l.

Table 14. Results[a] of the randomization test for comparing variances: Maxillary dentition.

s_f^2	reference	s_r^2	ln (s_f^2/s_r^2)	c	p
P^3 b-l					
0.0048	*A. robustus*	0.0024	0.6786	129	0.130
	Pan	0.0061	-0.2372	668	0.669
	Gorilla	0.0037	0.2545	264	0.265
P^4 b-l					
0.0039	*A. robustus*	0.0029	0.2961	273	0.274
	Pan	0.0037	0.0625	412	0.413
	Gorilla	0.0040	-0.0133	434	0.435
M^1 b-l					
0.0033	*A. robustus*	0.0019	0.5615	182	0.183
	Pan	0.0026	0.2480	266	0.267
	Gorilla	0.0045	-0.3107	656	0.657
M^2 b-l					
0.0094	*A. robustus*	0.0029	1.1942	42	0.043
	Pan	0.0040	0.8663	47	0.048
	Gorilla	0.0060	0.4547	164	0.165
M^3 b-l					
0.0091	*A. robustus*	0.0015	1.8275	1	0.001
	Pan	0.0044	0.7251	17	0.018
	Gorilla	0.0062	0.3772	176	0.177

[a] s_f^2 = variance of log-transfomed measurements for early *Homo*; s_r^2 = variance of log-transfomed measurements for reference samples; ln (s_f^2/s_r^2) = log of the ratio of s_f^2 and s_r^2, values > 1 indicate that the variance is greater in early *Homo* and values < 1 indicate that the variance is greater in the reference species; c = number of randomized log variance ratios equal to or greater than 1.

Table 15. Results of Levene's median ratio test for relative variation: Maxillary dentition.

reference species	fossil mean - reference mean	*t*	*p*
P^3 b-l: $F_{3,93} = 1.22$, $p=0.307$			
A. robustus	0.012	0.69	0.246
Pan	-0.101	-0.64	0.762
Gorilla	0.004	0.25	0.402
P^4 b-l: $F_{3,97} = 0.14$, $p=0.813$			
A. robustus	0.004	0.24	0.404
Pan	-0.003	-0.21	0.916
Gorilla	<0.001	-0.01	0.999
M^1 b-l: $F_{3,104} = 1.42$, $p=0.241$			
A. robustus	0.014	1.10	0.137
Pan	0.006	0.50	0.308
Gorilla	-0.006	-0.53	0.799
M^2 b-l: $F_{3,95} = 1.73$, $p=0.165$			
A. robustus	0.034	1.74	0.043
Pan	0.026	1.38	0.085
Gorilla	0.012	0.64	0.262
M^3 b-l: $F_{3,98} = 3.99$, $p=0.010$			
A. robustus	0.044	2.80	0.003
Pan	0.020	1.35	0.090
Gorilla	0.012	0.79	0.216

Table 16. Results of Levene's median log test for relative variation: Maxillary dentition.

reference species	fossil mean - reference mean	*t*	*p*
P^3 b-l: $F_{3,93} = 1.23$, $p=0.304$			
A. robustus	0.012	0.70	0.243
Pan	-0.010	-0.64	0.762
Gorilla	0.004	0.24	0.404
P^4 b-l: $F_{3,97} = 0.10$, $p=0.960$			
A. robustus	0.004	0.27	0.395
Pan	-0.002	-0.12	0.953
Gorilla	<0.001	<-0.01	0.999
M^1 b-l: $F_{3,104} = 1.36$, $p=0.258$			
A. robustus	0.015	1.18	0.120
Pan	0.006	0.52	0.300
Gorilla	-0.005	-0.42	0.838
M^2 b-l: $F_{3,95} = 1.60$, $p=0.196$			
A. robustus	0.028	1.45	0.075
Pan	0.021	1.14	0.128
Gorilla	0.006	0.33	0.372
M^3 b-l: $F_{3,98} = 4.15$, $p=0.008$			
A. robustus	0.044	2.84	0.003
Pan	0.020	1.39	0.084
Gorilla	0.011	0.77	0.220

CHAPTER 8

MULTIVARIATE RESULTS: THE MAGNITUDE AND PATTERN OF CRANIOMETRIC VARIATION IN EARLY *HOMO*

In this chapter the results of the multivariate comparisons of KNM-ER 1470 with KNM-ER 1805, 1813 and OH 24 are presented. For the comparisons between KNM-ER 1470 and 1813, and KNM-ER 1470 and OH 24 the results of the analyses based on the calvarial measurements are presented first, followed by the results for the comparisons of the faces. The comparison of KNM-ER 1470 with 1805 is based only on measurements of the vault. For each comparison the differences between the fossils are first contrasted with the differences between individuals in the modern referents, followed by comparisons with the multivariate distances between other Plio-Pleistocene hominids. The purpose of the latter is to determine how the distances between early *Homo* crania compare to the distances between fossil hominids which are generally considered to belong to the same species, as well as how they compare to distances between fossils which undoubtedly represent different species. Because of the fragmentary and incomplete condition of the fossil crania, these latter comparisons are by necessity based on a smaller set of measurements. The results of the phenetic comparisons of the early *Homo* specimens with other Plio-Pleistocene hominids are presented in the following chapter.

KNM-ER 1470 and KNM-ER 1813

The magnitude and pattern of variation in the vault

Comparisons with modern hominoids

For the vault the results of the comparisons of the Mahalanobis, shape and size distances between KNM-ER 1470 and 1813 with the equivalent distances between all possible pairs of individuals in the reference samples are given in Table 17. These comparisons are based on 12 measurements: GOL, GBC, GBA, MFB, PAC, PAA, BSC, SPC, ASB, LAC, XPB and POB.

TABLE 17. Descriptive statistics and results[a] of the multivariate distance comparisons based on calvarial measurements: KNM-ER 1470 - KNM-ER 1813. Variables used: GOL, GBC, GBA, MFB, PAC, PAA, BSC, SPC, ASB, LAC, XPB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance	c_{ff}	c_{mf}	c_{mm}	*c*	*p*
Mahalanobis Distances - distance between KNM-ER 1470 and KNM-ER 1813 = 48.96										
Homo	4371	12.84	43.92	107.19	141.74	100	106	0	206	0.0474
Pan	2346	20.29	44.39	57.61	97.74	12	49	15	76	0.0328
Pongo	946	26.77	49.36	61.28	64.91	4	37	11	52	0.0560
Gorilla	3486	27.99	58.57	89.34	124.64	43	254	83	380	0.1093
Shape Distances - distance between KNM-ER 1470 and KNM-ER 1813 = 38.05										
Homo	4371	12.10	42.53	105.68	141.17	120	112	0	232	0.0533
Pan	2346	18.79	42.54	57.16	97.20	33	103	36	172	0.0737
Pongo	946	24.58	46.91	56.97	62.20	30	80	29	139	0.1480
Gorilla	3486	23.73	52.58	85.35	114.70	67	307	180	554	0.1592
Size Distances - distance between KNM-ER 1470 and KNM-ER 1813 = 10.91										
Homo	4371	0.36	2.65	4.21	6.43	0	0	0	0	0.0002
Pan	2346	0.70	4.91	7.58	9.92	0	0	0	0	0.0004
Pongo	946	0.96	7.22	11.11	16.35	0	10	0	10	0.0116
Gorilla	3486	2.24	13.7	20.52	35.98	2	311	12	325	0.0935

[a] *np* = number of pairwise comparisons; c_{ff} = number of female-female distances ≥ distance between fossils; c_{mf} = number of male-female distances ≥ distance between fossils; c_{mm} = number of male-male distances ≥ distance between fossils; *c* = total number of pairwise distances between individuals ≥ distance between fossils.

In Figure 3 the Mahalanobis D^2 between the fossils is compared with the distributions of pairwise D^2s between individuals in the modern *Homo*, *Pan*, *Pongo* and *Gorilla* samples. For each distribution the vertical line shows the position of the distance between KNM-ER 1470 and 1813, and the p is the probability of equalling or exceeding that distance in the reference sample. The results in Table 17 and Figure 3 show that the Mahalanobis distance between KNM-ER 1470 and 1813 (48.96), is relatively quite large, although it is within the range of distances found in all of the reference samples. The probability of seeing a distance of this magnitude between two individuals from a species as sexually dimorphic as modern *Homo*, *Pan* or *Pongo* is small, but it is somewhat more likely that the fossils could represent a single species if that species were as dimorphic as *Gorilla*. The observed D^2 between the fossils is greater than most of the pairwise distances seen in the modern human reference sample, for which the median distance is 12.84. Of the 4371 possible pairwise distances in this sample only 206 equal or exceed the observed distance between the fossils and the p-value of 0.0474 indicates that for a species as sexually dimorphic as modern humans the probability of randomly sampling two individuals which are as different from one another as KNM-ER 1470 and 1813 is quite small. For the *Pan* sample there are 2346 possible pairwise comparisons. The median distance in this sample is 20.29 and only 76 of the distances are equal to or greater than the distance between the fossils ($p = 0.0328$). For the smaller orangutan sample, with a median D^2 of 26.77, there are 946 possible distances, 52 of which are greater than or equal to the Mahalanobis D^2 between the fossils, and the probability of matching or exceeding the observed D^2 in this sample is only 0.0560. Even when compared to the distribution of pairwise D^2s within the very dimorphic *Gorilla* sample (median D^2 = 27.99) the distance between the fossils is relatively large. Of the 3486 distances between gorillas 380 are equal to or greater than the D^2

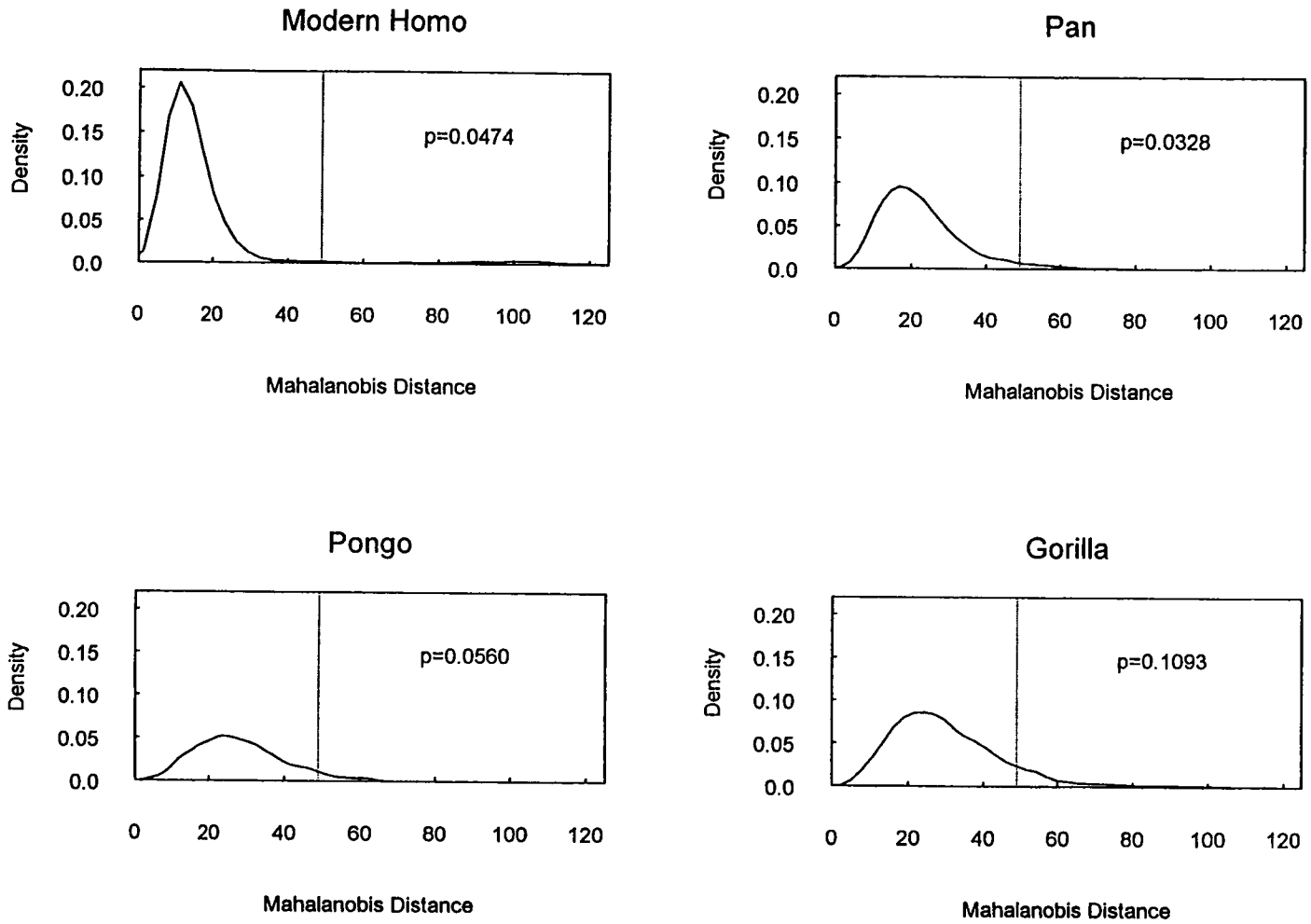


Figure 3. The smoothed distributions of all possible Mahalanobis distances between individuals in the reference samples plotted against the Mahalanobis distance between KNM-ER 1470 and KNM-ER 1813 for the vault. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

between the fossils and the *p*-value of 0.1093 indicates that the probability of sampling two individuals as different as KNM-ER 1470 and 1813 from a species as dimorphic as *Gorilla* is relatively small.

The results given in Table 17 suggest that if KNM-ER 1470 and 1813 do represent the same species they could be of the same or opposite sex, although the latter is more likely. In all of the reference samples the number of males and females is approximately equal and consequently about half of all pairwise comparisons are between males and males, or females and females, and about half are between males and females. If the differences between the fossils do not reflect sexual dimorphism the number of opposite-sex and same-sex pairwise distances equal to or greater than the distance between the fossils should have approximately the same proportions. For the modern human sample 100 of the 206 distances that equal or exceed the observed D^2 are between females and females and 106 are between males and females. None of the distances between males are greater than the distance between the fossils. These unusual proportions seem peculiar and may possibly be due to an incorrect identification of a male, or perhaps more than one male, as female in the collection records. In the chimpanzee sample the observed D^2 between the fossils is exceeded by distances between males and males, females and females and males and females, but a disproportionate number of these are between males and females. Of the 76 pairwise distances greater than or equal to the observed D^2 49 (65%) are between male-female pairs and only 27 are between females and females or males and males. For the orangutan reference sample there are 52 pairwise distances that equal or exceed the D^2 between KNM-ER 1470 and 1813. Thirty seven (71%) of these are between males and females and only 15 female-female and male-male distances match or exceed the distance between the fossils. Approximately 67% (254) of the 380 pairwise distances in the gorilla sample that are greater than or equal to the distance between the fossils are between opposite-sex pairs.

The differences between the KNM-ER 1470 and 1813 in the shape of the vault also appear to be rather large relative to the shape differences seen in modern hominoids. The results of the shape comparisons are presented in Table 17, and the distributions of all possible pairwise shape distances in the reference samples are shown in Figure 4. The observed shape D^2 between KNM-ER 1470 and 1813 of 38.05 is within the ranges of shape distances seen in all of the reference groups, but it falls in the upper tail of all four distributions. However, the probabilities for the observed shape D^2 are not as small as those for the Mahalanobis D^2. In the modern human distribution of 4371 distances 232 are equal to or greater than the observed distance, and the probability of finding a distance of this magnitude or greater in the modern human sample is 0.0533. For the distribution of shape distances in the *Pan* reference sample a total of 172 out of 2346 shape D^2s equal or exceed the distance between KNM-ER 1470 and 1813, and the probability of exceeding the observed D^2 in the chimpanzee sample is 0.0737. In the more dimorphic *Pongo* and *Gorilla* samples a larger number of distances exceed the distance between the fossils. In the distribution of 946 distances between orangutans 139 pairwise shape distances are greater than or equal to the observed shape D^2 ($p = 0.1480$). For the *Gorilla* sample 554 of the 3486 shape distances between individuals equal or exceed the observed shape D^2 ($p = 0.1592$). Overall the results of the comparisons of the shape distances indicate that the distance between KNM-ER 1470 and 1813 is unlikely to be seen in a species with the same degree of variation as modern humans or chimpanzees but the probability that the two fossils could represent the same species is much greater if that species were as dimorphic as orangutans or gorillas.

The results presented in Table 17 show that if KNM-ER 1470 and 1813 do represent the same species the shape differences between them could be found between individuals of the same or opposite sex. In the modern human sample 232 shape distances exceed the observed shape D^2 between the fossils. Nearly half (112) of these are between males and

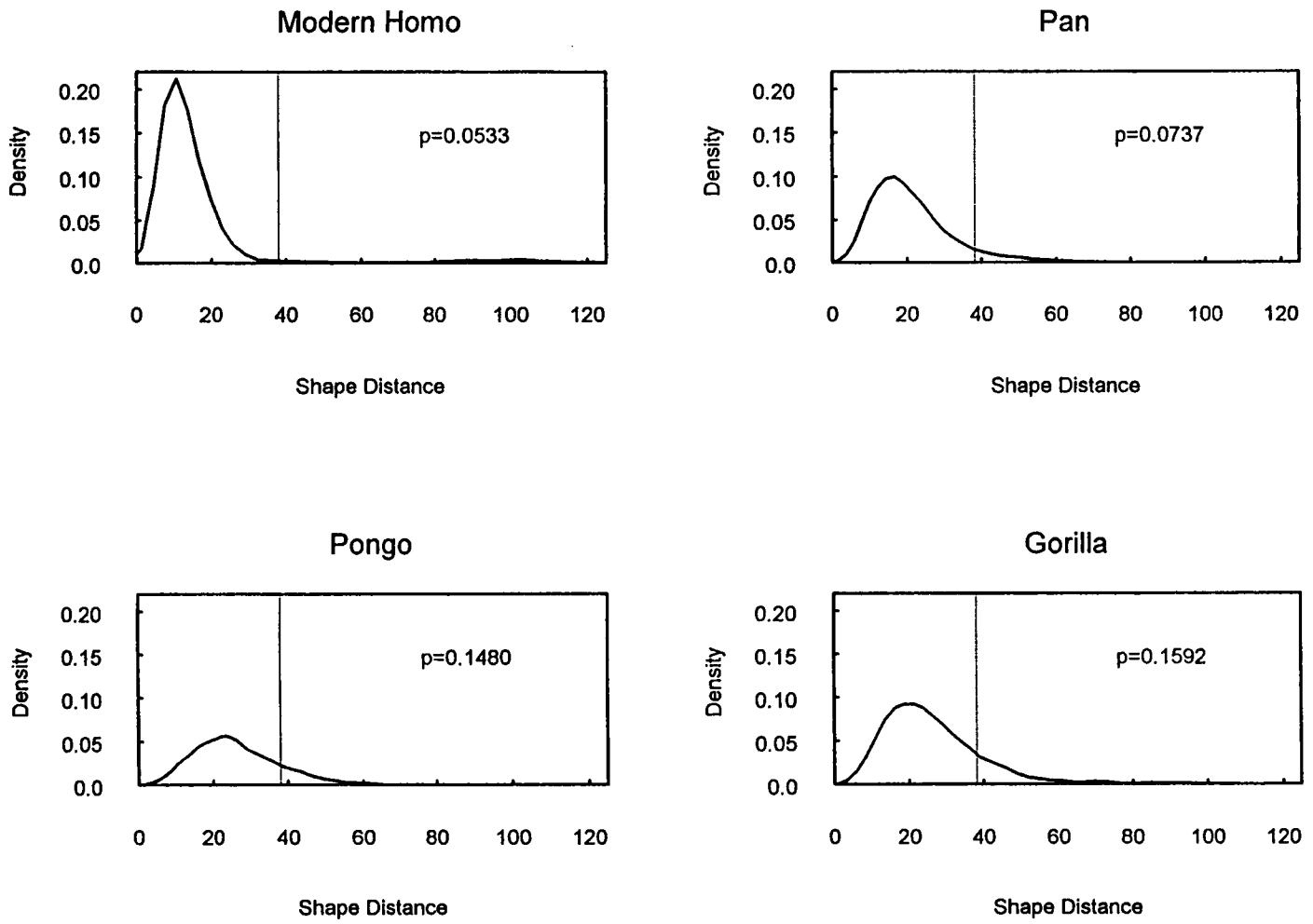


Figure 4. The smoothed distributions of all possible shape distances between individuals in the reference samples plotted against the shape distance between KNM-ER 1470 and KNM-ER 1813 for the vault. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

females, and the remaining distances are between females and females. In the chimpanzee sample 60% (103) of the 172 shape distances greater than or equal to the observed shape D^2 are between males and females and of the remaining 69 distances approximately half are between females and females and half are between males and males. Nearly the same proportions are seen in the orangutan sample where 57% (80 out of 139) of the pairwise distances greater than or equal to the observed shape distance are between male-female pairs and in the gorilla reference group 55% (307 out of 554) of the shape distances greater than or equal to the observed distance are between males and females.

The results in Table 17 show that for the vault the most striking difference between KNM-ER 1470 and 1813 is the disparity in size. The distributions of pairwise size distances between individuals in the modern human, *Pan*, *Pongo* and *Gorilla* samples are shown in Figure 5. Here it can be seen that the size distance between KNM-ER 1470 and 1813 of 10.91 is beyond the range of size distances seen in the modern human and chimpanzee samples. In the modern human sample the median size distance between individuals is only 0.36 and the largest size distance is 6.43. For the chimpanzee sample the median is only 0.70 and the maximum distance is 9.92. None of the pairwise distances between modern humans or between chimpanzees equals or exceeds the size D^2 between the fossils and thus, the probability of randomly sampling two individuals as disparate in size as KNM-ER 1470 and 1813 from a species as sexually dimorphic as modern humans or *Pan* is very small ($p = 0.0002$ and 0.0004, respectively). The observed size D^2 of 10.91 is also quite large relative to the size distances between individuals in the orangutan reference group. It is much larger than the median size distance (0.96) and in the distribution of 946 shape distances between orangutans only 10 are equal to or greater than the size D^2 between the fossils. The p-value of 0.0116 for this distance shows that even for a species as sexually dimorphic as *Pongo* the probability of finding two individuals as disparate in size as KNM-ER 1470 and 1813 is small. Even when compared to the most dimorphic reference group the

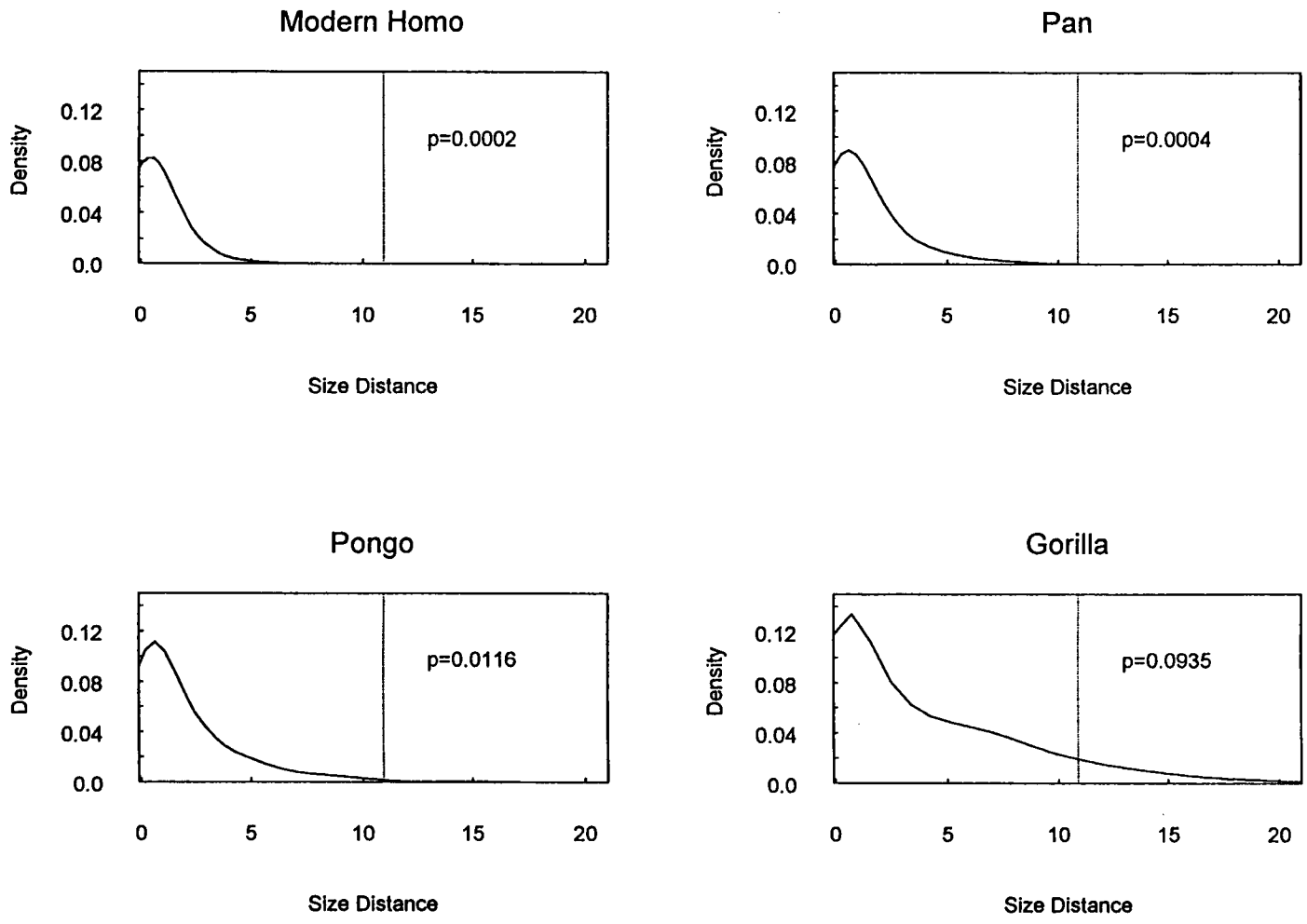


Figure 5. The smoothed distributions of all possible size distances between individuals in the reference samples plotted against the size distance between KNM-ER 1470 and KNM-ER 1813 for the vault. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

size difference between the fossils is relatively quite large. In the gorilla sample the median pairwise size distance is 2.24, and only 325 of the 3486 pairwise distances between individuals are greater than or equal to the size distance between KNM-ER 1470 and 1813 ($p = 0.0935$).

If KNM-ER 1470 and 1813 do represent a species as sexually dimorphic as *Pongo* or *Gorilla* the size differences between them are almost certainly due to sexual dimorphism. All of the 10 size distances in the orangutan sample that equal or exceed the size distance between the fossils are between males and females. In the gorilla sample only 2 distances between pairs of females and only 12 distances between pairs of males are greater than the size D^2 between the fossil crania; 96% of the size distances between gorillas that exceed the size distance between the fossils are between males and females.

Comparisons with Plio-Pleistocene hominids

The comparisons of the Mahalanobis, shape and size distances between the early *Homo* crania with the equivalent distances between other Plio-Pleistocene hominids are based on a smaller number of variables than the comparisons with modern hominoids. This is necessary to allow for the inclusion of as many fossil crania as possible. The comparisons of the differences in the vault between KNM-ER 1470 and 1813 are based on eight measurements (GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB) and, excluding KNM-ER 1470 and 1813, the Plio-Pleistocene hominid sample consists of 7 crania. Within this comparative sample there are 3 pairs of fossils that are most likely conspecific: the male and female *A. boisei* crania KNM-ER 406 and 407; Sts 5 and 71 (*A. africanus*); and KNM-ER 3733 and 3883 (*Homo erectus*). OH 24 is also included in the fossil sample, but it will be discussed below

The matrix of Mahalanobis D^2s between the fossil crania is given in Table 18, and for comparative purposes the descriptive statistics for the distributions of all pairwise Mahalanobis distances within the reference samples, based on the same set of measurements, are shown in Table 19. These provide a baseline with which the distances between the fossils

Table 18. Mahalanobis distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on eight calvarial measurements. Variables used: GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB.

	ER 1813	OH 24	ER 406	ER 407	Sts 5	Sts 71	ER 3733	ER 3883
ER 1470	29.29	17.98	67.94	37.12	38.11	50.52	16.67	15.80
ER 1813		28.99	80.79	35.87	25.88	70.10	43.18	56.41
OH 24			38.34	9.11	11.72	28.88	45.68	26.06
ER 406				22.05	40.24	40.62	136.96	92.12
ER 407					13.00	34.23	85.08	59.05
Sts 5						30.88	68.50	48.30
Sts 71							96.17	60.45
ER 3733								23.12

Table 19. Descriptive statistics for all pairwise Mahalanobis distances within the modern reference species based on eight calvarial measurements. Variables used: GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance
Homo	4371	6.97	38.27	102.44	132.93
Pan	2346	11.90	33.87	51.12	94.37
Pongo	946	17.55	35.86	44.13	49.39
Gorilla	3486	18.06	43.33	83.56	115.07

can be compared. The Mahalanobis distance between KNM-ER 1470 and 1813 of 29.29 exceeds the median distances in all of the reference groups, but it does not exceed any of the upper 95th percentiles. The distance between KNM-ER 1470 and 1813 is also larger than the Mahalanobis D^2 between the male and female *A. boisei* crania KNM-ER 406 and 407 (22.05), larger than the distance between the two *Homo erectus* specimens KNM-ER 3733 and 3883 (23.12), and approximately equal to the distance between the two *A. africanus* fossils, Sts 71 and Sts 5 (30.88). It should be noted that all of the Mahalanobis distances between pairs of fossils that most likely belong to the same species are smaller than the upper 95th percentile values seen in the modern reference groups.

The Mahalanobis distance between KNM-ER 1470 and 1813 is not as large as the distances between hominids that belong to different species. The distances between the *A. boisei* cranium KNM-ER 406 and the *A. africanus* and *Homo erectus* vaults are all considerably larger than the D^2 between KNM-ER 1470 and 1813 and the same is true for the distances between the *A. africanus* and the *Homo erectus* crania. For example, the Mahalanobis D^2 between KNM-ER 1470 and 1813 of 29.29 is smaller than the distances between KNM-ER 406 and Sts 5 or Sts 71 (40.24 and 40.62, respectively), or between Sts 5 and KNM-ER 3733 or 3883 (68.50 and 48.30, respectively) and much smaller than the D^2 between KNM-ER 406 and KNM-ER 3733 or 3883 (136.96 and 92.12, respectively). The distance between KNM-ER 1470 and 1813 is however, considerably larger than the distance between the female *A. boisei* cranium KNM-ER 407 and Sts 5 (13.00) and it is close to the distance between KNM-ER 407 and Sts 71(34.23).

For the shape comparisons the matrix of shape distances between Plio-Pleistocene hominids is shown in Table 20, and the descriptive statistics for the distributions of all pairwise shape distances in the reference samples are given in Table 21. The shape distance between KNM-ER 1470 and 1813 is 16.39, this is larger than the median distances in all of the reference groups but considerably smaller than the shape D^2s at the upper 95th

Table 20. Shape distances among KNMER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominid based on eight calvarial measurements. Variables used: GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB.

	ER 1813	OH 24	ER 406	ER 407	Sts 5	Sts 71	ER 3733	ER 3883
ER 1470	16.39	14.53	66.79	31.43	31.84	39.18	16.65	15.26
ER 1813		25.99	74.42	34.42	24.70	70.05	29.18	37.66
OH 24			37.71	8.83	11.30	26.60	41.65	19.31
ER 406				20.32	38.18	35.33	135.48	88.86
ER 407					12.98	33.27	78.65	49.28
Sts 5						30.13	61.46	37.78
Sts 71							83.80	43.58
ER 3733								22.78

Table 21. Descriptive statistics for all pairwise shape distances within the modern reference species based on eight calvarial measurements. Variables used: GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance
Homo	4371	6.34	34.79	100.79	132.12
Pan	2346	10.48	32.07	49.72	93.47
Pongo	946	15.38	32.25	40.61	47.01
Gorilla	3486	13.94	36.73	80.38	106.21

percentiles. The shape distance between KNM-ER 1470 and 1813 is also smaller than the shape distances between pairs of fossils derived from the same species. The shape D^2 between KNM-ER 406 and 407, which both represent *A. boisei*, equals 20.32; the shape distance between the *Homo erectus* crania KNM-ER 3733 and 3883 is 22.78; and the distance between the two *A. africanus* specimens, Sts 5 and Sts 71, is 30.13. All of these distances are smaller than the upper 95th percentile values in the reference distributions.

The shape distance between KNM-ER 1470 and 1813 is also much smaller than all but one of the distances between fossils that represent different species. The shape distances between the *A. boisei* and *Homo erectus* crania, between the *Homo erectus* and *A. africanus* crania and between the *A. boisei* skull KNM-ER 406 and the two *A. africanus* vaults, Sts 5 and Sts 71, are all larger than the distance between KNM-ER 1470 and 1813. Only the distance between ER 407 and Sts 5 is smaller.

In the comparisons with the modern hominoids the most striking difference between KNM-ER 1470 and 1813 is the disparity in size, and this marked disparity in size is also apparent when the size distance between these specimens is compared with the size distances between other Plio-Pleistocene hominid vaults. The matrix of size distances between the Plio-Pleistocene hominids is shown in Table 22, and the descriptive statistics for the distributions of size distances within the reference groups are given in Table 23. The size distance between KNM-ER 1470 and 1813 of 12.90 is very large relative to the pairwise size D^2s seen in the reference samples. It is larger than the maximum size distances in the modern *Homo* and *Pan* samples, larger than the upper 99th percentile of the *Pongo* distribution, and almost as large as the upper 95th percentile in the *Gorilla* distribution. The size distance of 12.90 is also much larger than the size distances between conspecific fossils. The size D^2 between KNM-ER 406 and 407 is 1.74, between Sts 5 and Sts 71 it is 0.75 and between KNM-ER 3733 and 3883 it is only 0.35. These distances are all smaller than the upper 95th percentile distances in the reference groups.

Table 22. Size distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominid based on eight calvarial measurements. Variables used: GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB.

	ER 1813	OH 24	ER 406	ER 407	Sts 5	Sts 71	ER 3733	ER 3883
ER 1470	12.90	3.46	1.14	5.70	6.28	11.35	0.02	0.55
ER 1813		3.00	6.38	1.45	1.18	0.05	13.99	18.75
OH 24			0.63	0.28	0.42	2.28	4.03	6.75
ER 406				1.74	2.06	5.29	1.48	3.27
ER 407					0.02	0.96	6.43	9.77
Sts 5						0.75	7.04	10.52
Sts 71							12.37	16.87
ER 3733								0.35

Table 23. Descriptive statistics for all pairwise size distances within the modern reference species based on eight calvarial measurements. Variables used: GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance
Homo	4371	0.35	2.69	4.61	7.16
Pan	2346	0.71	5.06	7.78	9.91
Pongo	946	1.03	7.37	11.81	18.03
Gorilla	3486	2.15	13.30	20.71	36.87

The distance between KNM-ER 1470 and 1813 is also larger than the size distances between the *A. boisei* and *Homo erectus* crania, larger than the size D^2s between the *A. boisei* and *A. africanus* vaults and larger than the distances between Sts 5 and KNM-ER 3733 or 3883. Only the size distances between Sts 71 and the two *Homo erectus* crania, KNM-ER 3733 and 3883, are as large as, or larger than, the distance between KNM-ER 1470 and 1813.

The magnitude of the size difference between KNM-ER 1470 and 1813 can be seen more easily in Figure 6, which shows the positions of the fossils along the single size dimension. This is found by using principal coordinates analysis to reduce the matrix of size distances between the fossils to a single axis of variation. Here it is quite apparent that the size difference between KNM-ER 1470 and 1813 is much larger than any of the differences between hominids belonging to the same species, i.e. Sts 5 and Sts 71, KNM-ER 3733 and 3883, or KNM-ER 406 and 407. It is also larger, in some cases much larger, than most of the size differences between fossils that represent different species.

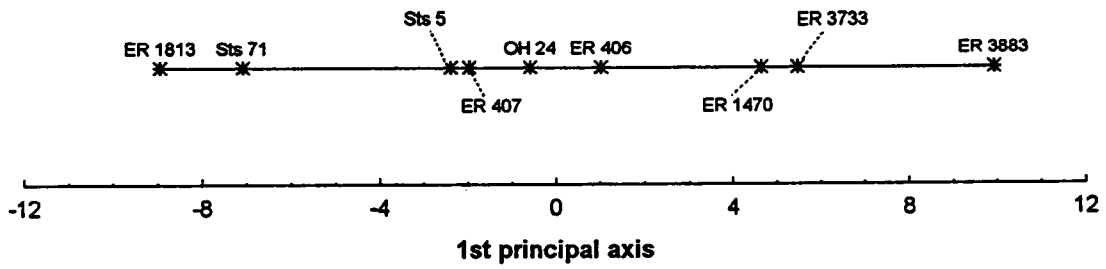


Figure 6. Size differences among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on calvarial measurements.

The magnitude and pattern of variation in the face

Comparisons with modern hominoids

The results of the multivariate comparisons of the differences between KNM-ER 1470 and 1813 in the face with the differences in the faces of modern hominoids are given in Table 24. These comparisons are based on 13 measurements: JUB, FMB, EKB, OBB, OBH, IOB, NLB, NLH, NPH, MMH, MAB, PLB and CCB.

In Figure 7 the Mahalanobis D^2 between KNM-ER 1470 and 1813 is compared with the distributions of pairwise D^2s between individuals in the modern *Homo*, *Pan*, *Pongo* and *Gorilla* samples. The results in Table 24 and Figure 7 demonstrate that the differences in the face are not as pronounced as the differences in the vault. The D^2 between the fossils is 24.47. This is much larger than the median distance of 12.76 for the modern *Homo* sample, but it is only slightly larger than the median distance for *Pan* (22.75) and it is smaller than the median distances in the orangutan and gorilla samples (27.76 and 27.42, respectively). The Mahalanobis D^2 between KNM-ER 1470 and 1813 is relatively large only when compared to the modern human distribution. In this reference sample 234 out of 3655 possible pairwise distances are equal to or greater than the distance between the fossils ($p = 0.0643$). For all three of the pongid samples the probability of finding a pairwise D^2 greater than or equal to the observed distance is quite large. In the distribution of 2415 pairwise distances in the chimpanzee reference group 1059 exceed or equal the observed distance between KNM-ER 470 and 1813 ($p = 0.4385$) and in the orangutan and gorilla reference groups the proportion of distances that are equal to or greater than the observed D^2 is even larger. In the *Pongo* sample 1217 out of 2016, and in the *Gorilla* sample 2121 out of 3486 distances match or exceed the distance between KNM-ER 1470 and 1813 ($p = 0.6042$ for *Pongo* and 0.6087 for *Gorilla*).

If KNM-ER 1470 and 1813 are conspecific the results presented in Table 24 suggest that for the face the differences between them do not necessarily reflect sexual dimorphism, the

TABLE 24. Descriptive statistics and results[a] of the multivariate distance comparisons based on facial measurements: KNM-ER 1470 - KNM-ER 1813. Variables used: JUB, FMB, EKB, OBB, OBH, IOB, NLB, NLH, NPH, MMH, MAB, PLB, CCB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance	c_{ff}	c_{mf}	c_{mm}	*c*	*p*
Mahalanobis Distances - distance between KNM-ER 1470 and KNM-ER 1813 = 24.47										
Homo	3655	12.76	25.68	34.55	47.62	62	118	54	234	0.0643
Pan	2415	22.75	50.51	72.58	96.04	272	575	212	1059	0.4385
Pongo	2016	27.76	50.37	60.31	78.99	291	716	210	1217	0.6042
Gorilla	3486	27.42	63.82	238.12	401.13	376	1269	476	2121	0.6087
Shape Distances - distance between KNM-ER 1470 and KNM-ER 1813 = 16.88										
Homo	3655	12.16	24.87	33.88	47.23	213	453	181	847	0.2320
Pan	2415	21.64	49.08	71.81	95.95	488	868	321	1677	0.6944
Pongo	2016	23.78	45.81	56.75	70.55	481	783	272	1536	0.7624
Gorilla	3486	24.24	60.81	233.95	393.62	619	1423	680	2722	0.7811
Size Distances - distance between KNM-ER 1470 and KNM-ER 1813 = 7.59										
Homo	3655	0.28	2.09	3.33	5.72	0	0	0	0	0.0003
Pan	2415	0.51	3.97	6.43	11.22	2	4	2	8	0.0037
Pongo	2016	1.70	12.49	18.22	23.65	4	267	17	288	0.1434
Gorilla	3486	1.66	11.11	14.97	20.20	0	474	0	474	0.1363

[a] np = number of pairwise comparisons; c_{ff} = number of female-female distances ≥ distance between fossils; c_{mf} = number of male-female distances ≥ distance between fossils; c_{mm} = number of male-male distances ≥ distance between fossils; c = total number of pairwise distances between individuals ≥ distance between fossils.

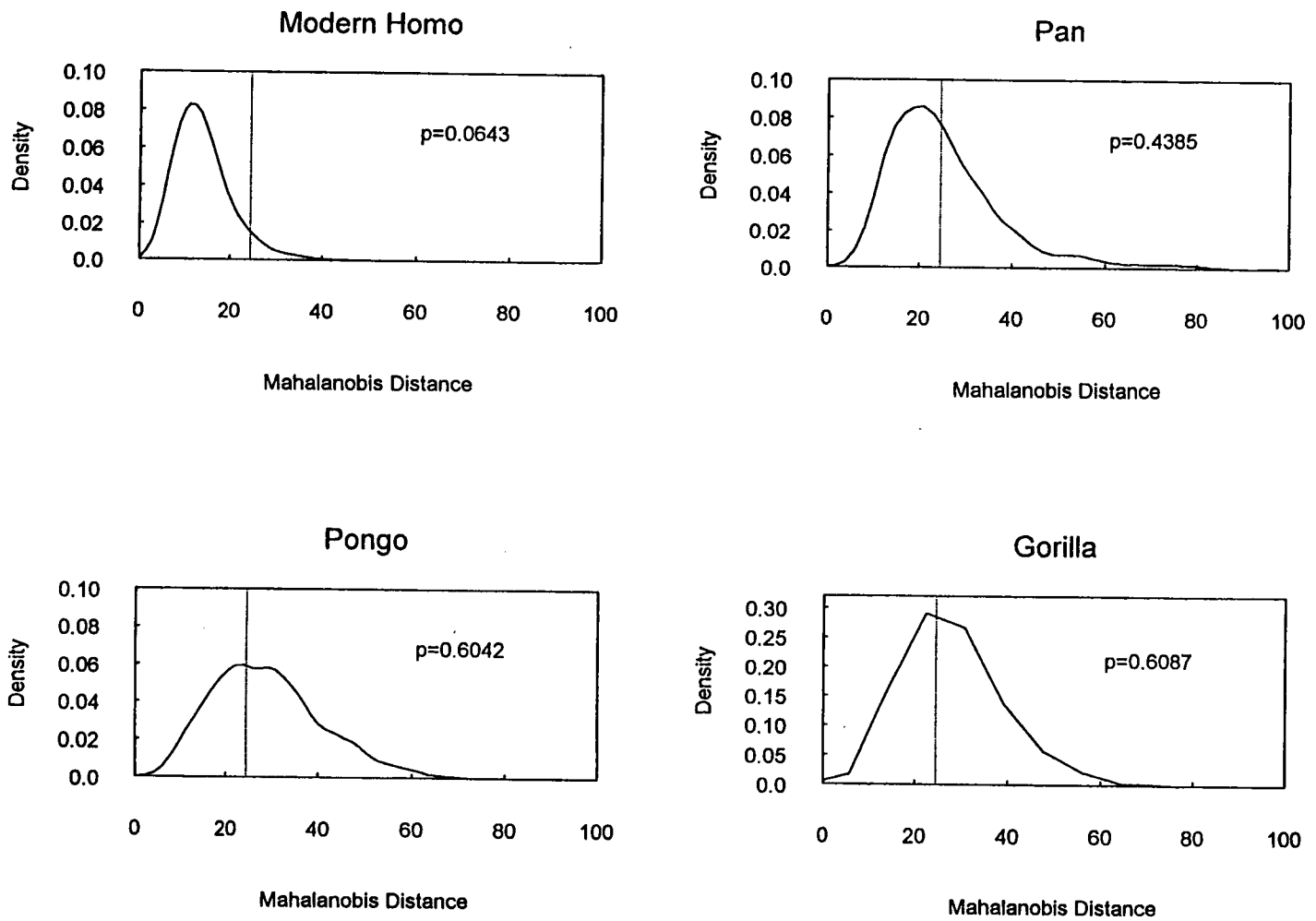


Figure 7. The smoothed distributions of all possible Mahalanbois distances between individuals in the reference samples plotted against the Mahalanobis distance between KNM-ER 1470 and KNM-ER 1813 for the face. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

two could be of the same sex. In all of the reference samples the D^2 between the fossils is exceeded or equalled by distances between males and females, males and males, and females and females and in all of the reference groups approximately half of these distances are between males and females. In the modern *Homo* sample 50% (118 out of 234) of the distances equal to or greater than the observed D^2 are between males and females. In the chimpanzee sample 54% (575 out of 1059) of these distances are between males in females and in the orangutan and gorilla samples a slightly larger percentage (59% for *Pongo* and 60% for *Gorilla*) of the distances greater than or equal to the D^2 between the fossils are between males and females.

The results in Table 24 also show that the shape differences between the faces of KNM-ER 1470 and 1813 are not unusually large. In all of the reference groups a large number of pairwise distances equal or exceed the distance between KNM-ER 1470 and 1813, and the probability that the shape distance between the fossils could be matched or exceeded in any of the reference groups is large. This is evident in Figure 8 where the distributions of all possible pairwise shape D^2s in the reference samples are shown. The shape distance between KNM-ER 1470 and 1813 is 16.88. This value is larger than the median shape distance of 12.16 for modern *Homo*, but much smaller than the value at the upper 95th percentile. In the modern human sample 847 of the 3655 pairwise distances are equal to or greater than the distance between the fossils ($p=0.2320$). The shape D^2 between KNM-ER 1470 and 1813 is less than the median distances in all three pongid samples. In the distribution of shape distances between chimpanzees 1677 of the 2415 possible pairwise distances match or exceed the shape distance between the fossils ($p=0.6944$). For the *Pongo* sample 1536 of the 2016 possible pairwise distances are greater than or equal to the distance between KNM-ER 1470 and 1813 ($p=0.7624$) and for the *Gorilla* sample 2722 of the 3486 pairwise distances between individuals are equal to or surpass this distance ($p=0.7811$).

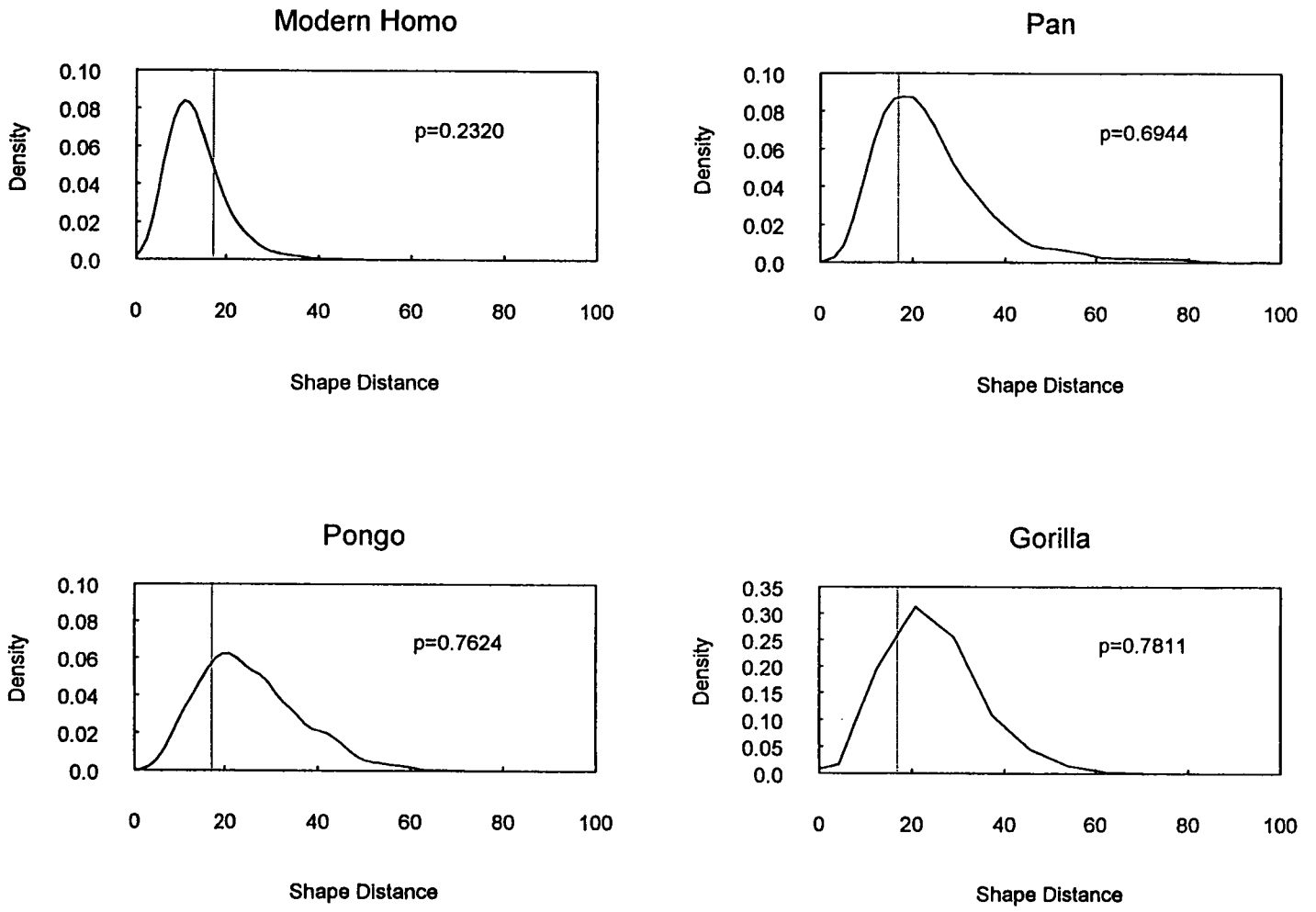


Figure 8. The smoothed distributions of all possible shape distances between individuals in the reference samples plotted against the size distance between KNM-ER 1470 and KNM-ER 1813 for the face. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

The results of the shape comparisons show that if KNM-ER 1470 and 1813 represent a single species, the differences between them in the shape of the face need not be due to sexual dimorphism. In all four reference groups approximately 50% of the shape distances between individuals that match or exceed the distance between the fossils are between males and females.

Figure 9 shows the distributions of facial size distances between all possible pairs of individuals in each of the reference groups. The results in Table 24 and Figure 9 demonstrate that although the Mahalanobis and shape distances between the faces of KNM-ER 1470 and 1813 are not unusually large, there is a marked disparity in the size of the face, particularly when the fossils are compared with the less dimorphic species. For the face the size distance between KNM-ER 1470 and 1813 is 7.59. This distance is greater than any of the size distances seen in the modern humans. The maximum size distance in the modern human distribution is only 5.72, and the probability that the size distance between KNM-ER 1470 and 1813 could be matched or equalled in a species as dimorphic as modern humans is very small ($p=0.0003$). The probability of equalling or exceeding the size distance between the fossils in a species as dimorphic as *Pan* is also small. In the distribution of 2415 pairwise size distances between chimpanzees only 8 are equal to or greater than the distance between the fossils ($p=0.0037$). Relative to the more dimorphic apes *Pongo* and *Gorilla* the size difference between KNM-ER 1470 and 1813 is not as extreme, and in the distributions of size distances for these species a larger proportion of the size distances are equal to or greater than the distance between the fossils. In the orangutan distribution 288 out of 2016, and in the gorilla distribution 474 out of 3486 distances equal or exceed the size distance between KNM-ER 1470 and 1813 ($p=0.1434$ for *Pongo* and 0.1363 for *Gorilla*).

For *Pan* 50% (4 out of 8) of the size D^2s greater than or equal to the distance between KNM-ER 1470 and 1813 are between males and females, but in the orangutan sample 95%

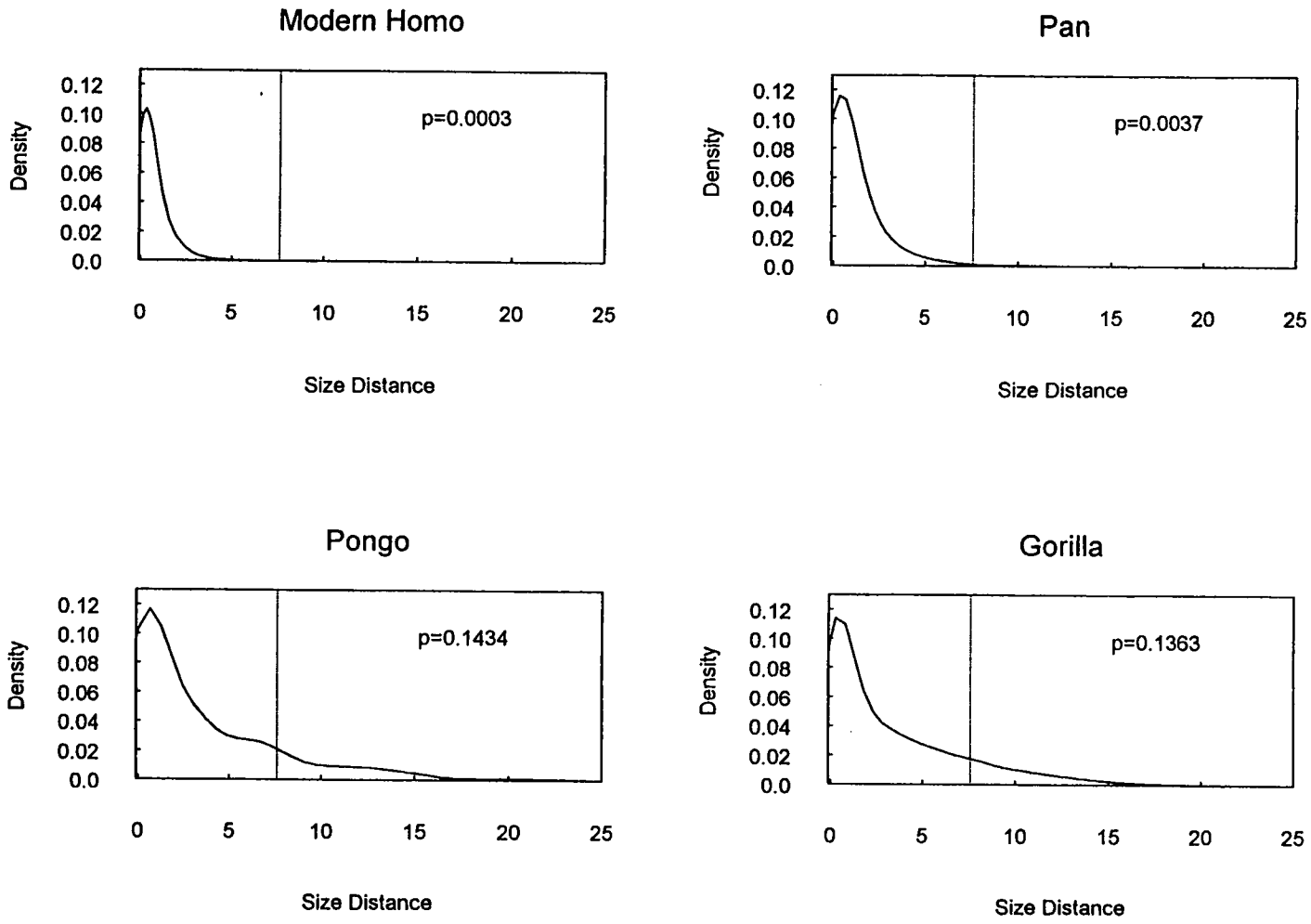


Figure 9. The smoothed distributions of all possible size distances between individuals in the reference samples plotted against the size distance between KNM-ER 1470 and KNM-ER 1813 for the face. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

(267 out of 288) and in the gorilla sample all of the distances that match or exceed the size distance between the fossils are between males and females. Thus, if KNM-ER 1470 and 1813 do represent a species as dimorphic as *Pongo* or *Gorilla*, the larger KNM-ER 1470 is most likely a male and KNM-ER 1813 is most likely a female.

Comparisons with Plio-Pleistocene hominids

For the face the multivariate comparisons of the differences between KNM-ER 1470 and 1813 with the differences between other Plio-Pleistocene hominids are based on 11 measurements: FMB, EKB, OBB, OBH, IOB, NLB, NLH, MMH, MAB and PLB. Excluding KNM-ER 1470 and 1813, the fossil hominid sample consists of 6 fossils. In this sample there are two pairs of fossils which are probably conspecific: KNM-ER 406 and OH 5, which represent *A. boisei*, and Sts 5 and 71, which represent *A. africanus*. OH 24 is also included in the fossil hominid sample, but it will be discussed below.

Overall the results of these comparisons are very similar to the comparisons with the modern hominoids. The matrix of Mahalanobis distances between Plio-Pleistocene hominids is shown in Table 25, and the descriptive statistics for the distributions of all pairwise Mahalanobis distances in the reference samples, based on the same set of measurements, are presented in Table 26. The Mahalanobis D^2 between KNM-ER 1470 and 1813 is 24.36. This is relatively large when compared to the distances in the modern human sample, it is greater than the upper 95th percentile, but smaller than the upper 99th percentile for this sample, but it is not large when compared to the pongid reference samples. It is somewhat larger than the median distances for *Pan*, *Pongo* and *Gorilla*, but much smaller than the D^2 values at the upper 95th percentiles. The distance between KNM-ER 1470 and 1813 is also smaller than the distances between conspecific fossil hominids. The D^2 between the *A. boisei* males KNM-ER 406 and OH 5, is 38.98 and the distance between the two *A. africanus* faces Sts 5 and Sts 71 is 26.61. The D^2 between KNM-ER 1470 and 1813 is also considerably smaller than the distances between fossils that belong to different species.

Table 25. Mahalanobis distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on eleven facial measurements. Variables used: FMB, EKB, OBB,OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB.

	ER 1813	OH 24	ER 406	OH 5	Sts 5	Sts 71	ER 3733
ER 1470	24.36	40.45	22.44	24.18	37.98	39.34	56.94
ER 1813		14.01	43.19	52.90	22.67	33.53	62.24
OH 24			59.62	86.82	37.43	47.22	85.53
ER 406				38.98	35.78	46.13	42.78
OH 5					32.72	46.62	67.77
Sts 5						26.61	62.56
Sts 71							110.90

Table 26. Descriptive statistics for all pairwise Mahalanobis distances within the modern reference species based on eleven facial measurements. Variables used: FMB, EKB, OBB, OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB.

reference species	*np*	median distance	upper 95th percentile	upper 99th perecentile	maximum distance
Homo	3655	10.10	21.58	29.86	45.61
Pan	2415	19.29	43.73	66.17	88.33
Pongo	2016	23.09	43.96	52.31	61.96
Gorilla	3486	22.50	56.05	234.77	391.25

The largest distance between fossils that are not conspecific is the distance of 110.90 between Sts 71(*A. africanus*) and KNM-ER 3733 (*H. erectus*), and the smallest D^2 between different species is the distance of 32.72 between the OH 5 (*A. boisei*) and Sts 5 (*A. africanus*).

Comparisons of the shape distance between KNM-ER 1470 and 1813 with the shape D^2s between other Plio-Pleistocene hominids indicate that the shape differences between the former are not unusually large. The matrix of shape D^2s between Plio-Pleistocene hominid faces is given in Table 27 and the descriptive statistics for the shape distances in the modern hominoid samples are shown in Table 28. The shape distance between KNM-ER 1470 and 1813 of 16.81 is not unusually large relative to the shape distances seen in the modern reference groups. It is larger than the median distance but smaller than the upper 95th percentile in modern *Homo* and it is smaller than the median distances in *Pan*, *Pongo* and *Gorilla*. The distance between KNM-ER 1470 and 1813 is also relatively small when compared to the shape distances between Sts 5 and 71 (26.54) and KNM-ER 406 and OH 5 (37.97). All of the distances between fossils that represent different species are greater than the distance between KNM-ER 1470 and 1813. The largest shape D^2 between fossils representing different species is the distance of 108.07 between Sts 71 and KNM-ER 3733, and the smallest distance between different species is the shape D^2 of 20.76 between OH 5 and Sts 5.

The matrix of size distances for the fossil hominids is shown in Table 29, and the descriptive statistics for the size distances in the extant reference samples are given in Table 30. Unlike the Mahalanobis and shape distances, the size distance between KNM-ER 1470 and 1813 (7.56) is large for two individuals who belong to the same species. This distance is greater than the maximum distance in the modern human sample and exceeds the upper 95th percentile in the chimpanzee distribution, but it is not as extreme when compared with the more dimorphic *Pongo* and *Gorilla* samples. Although it is considerably larger than the

Table 27. Shape distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on eleven facial measurements. Variables used: FMB, EKB, OBB,OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB.

	ER 1813	OH 24	ER 406	OH 5	Sts 5	Sts 71	ER 3733
ER 1470	16.81	35.23	22.43	23.43	31.53	34.16	56.58
ER 1813		13.79	36.09	39.45	22.63	33.31	57.99
OH 24			54.78	76.57	37.36	47.22	82.68
ER 406				37.97	29.75	41.32	42.52
OH 5					20.76	36.42	65.48
Sts 5						26.54	58.78
Sts 71							108.07

Table 28. Descriptive statistics for all pairwise shape distances within the modern reference species based on eleven facial measurements. Variables used: FMB, EKB, OBB, OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB.

reference species	*np*	median distance	upper 95th percentile	upper 99th perecentile	maximum distance
Homo	3655	9.47	20.74	29.35	45.28
Pan	2415	18.06	42.37	65.65	88.32
Pongo	2016	19.20	39.63	48.27	60.48
Gorilla	3486	19.32	53.40	231.49	385.65

Table 29. Size distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on eleven facial measurements. Variables used: FMB, EKB, OBB,OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB.

	ER 1813	OH 24	ER 406	OH 5	Sts 5	Sts 71	ER 3733
ER 1470	7.56	5.21	0.01	0.84	6.45	5.18	0.35
ER 1813		0.22	7.10	13.45	0.04	0.22	4.64
OH 24			4.84	10.25	0.07	> 0.01	2.85
ER 406				1.00	6.03	4.81	0.26
OH 5					11.96	10.21	2.29
Sts 5						0.07	3.78
Sts 71							2.83

Table 30. Descriptive statistics for all pairwise size distances within the modern reference species based on eleven facial measurements. Variables used: FMB, EKB, OBB, OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB.

reference species	*np*	median distance	upper 95th percentile	upper 99th perecentile	maximum distance
Homo	3655	0.30	2.21	3.45	6.10
Pan	2415	0.54	4.08	6.65	10.91
Pongo	2016	1.71	12.37	17.72	25.45
Gorilla	3486	1.63	10.75	14.64	19.00

median size distances in these samples the distance between the early *Homo* faces is smaller than the distances at the upper 95th percentiles. The size D^2 between KNM-ER 1470 and 1813 of 7.56 is much larger than the size distances between KNM-ER 406 and OH 5 (1.00) and Sts 5 and 71 (0.07). It also exceeds many of the size distances between fossils that represent different species. It is larger than the size distances between KNM-ER 3733 and Sts 5 or 71 (3.78 and 2.83, respectively), and it is larger than the size D^2 between KNM-ER 406 and Sts 5 or Sts 71 (6.03 and 4.81). Only the size distances between OH 5, which has a very large face, and the two gracile australopithecines are larger (11.96 and 10.21).

In Figure 10 the fossils are shown plotted along the single dimension of size variation. In this figure the size distance between KNM-ER 1470 and 1813 appears to be very large. It is greater than the distances between OH 5 and KNM-ER 406 or KNM-ER 3733, between Sts 5 or Sts 71 and KNM-ER 3733, and between Sts 5 or Sts 71 and KNM-ER 406. The size distance between KNM-ER 1470 and 1813 is exceeded only by the size distances between OH 5 and Sts 5 and 71.

KNM-ER 1470 and KNM-ER 1805

The magnitude and pattern of variation in the vault

The comparisons between KNM-ER 1470 and 1805 are based only on measurements of the cranial vault. Because KNM-ER 1805 is missing the anterior part of the frontal measurements of frontal length cannot be taken and these comparisons are based on a smaller number of variables than the comparisons between KNM-ER 1470 and 1813. Nine variables are used: MFB, PAC, PAA, BSC, SPC, ASB, LAC, XPB and POB.

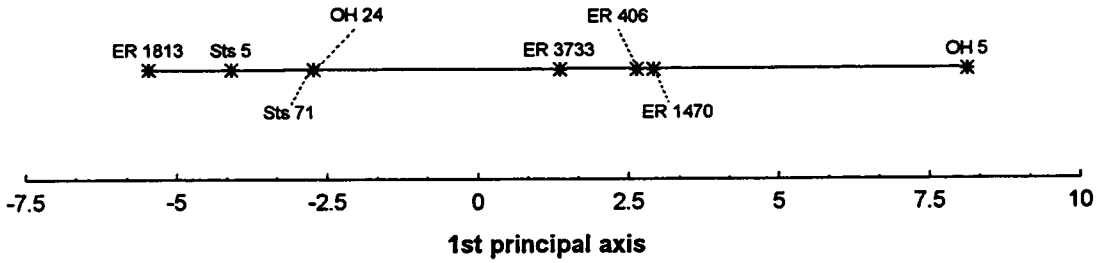


Figure 10. Size differences among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on facial measurements.

Comparisons with modern hominoids

The results of the comparisons of the multivariate differences between KNM-ER 1470 and 1805 with the differences between individuals in the modern reference samples are shown in Table 31. Overall, these results are very similar to the results of the comparisons between KNM-ER 1470 and 1813 for the vault. Figure 11 shows the distributions of all possible Mahalanobis D^2s in the reference groups. The Mahalanobis D^2 between KNM-ER 1470 and 1805 of 44.74 is within the range of distances found in all of the reference species, but it is relatively large, even for a dimorphic species such as *Gorilla*. The D^2 between KNM-ER 1470 and 1805 is above the 99th percentile for the modern *Homo* sample, and the probability of sampling two individuals that are as different from one another as KNM-ER 1470 and 1805 is very small for a species as dimorphic as modern humans: out of the 4371 pairwise comparisons between modern humans only 10 yield distances equal to or greater than the distance between the fossils ($p = 0.0025$). For the distribution of pairwise Mahalanobis distances in the chimpanzee sample the distance between the fossils falls between the upper 95th and 99th percentiles. In this distribution 61 of the 2346 pairwise

TABLE 31. Descriptive statistics and results[a] of the multivariate distance comparisons based on calvarial measurements: KNM-ER 1470 - KNM-ER 1805. Variables used: MFB, PAC, PAA, BSC, SPC, ASB, LAC, XPB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance	c_{ff}	c_{mf}	c_{mm}	*c*	*p*
Mahalanobis Distances - distance between KNM-ER 1470 and KNM-ER 1805 = 44.74										
Homo	4371	8.94	20.18	35.14	56.53	5	5	0	10	0.0025
Pan	2346	15.24	35.51	52.11	89.92	6	39	16	61	0.0264
Pongo	946	20.78	44.23	53.53	61.73	1	32	10	43	0.0465
Gorilla	3486	22.20	50.87	86.13	123.45	43	191	63	297	0.0855
Shape Distances - distance between KNM-ER 1470 and KNM-ER 1805 = 34.21										
Homo	4371	8.23	19.13	33.17	56.44	18	25	0	43	0.0101
Pan	2346	14.07	33.34	51.76	87.28	12	68	28	108	0.0465
Pongo	946	18.84	40.06	48.97	58.82	10	49	21	80	0.0856
Gorilla	3486	18.40	44.89	83.25	111.81	52	224	140	416	0.1196
Size Distances - distance between KNM-ER 1470 and KNM-ER 1805 = 10.54										
Homo	4371	0.35	2.55	3.94	7.04	0	0	0	0	0.0002
Pan	2346	0.64	4.82	7.68	12.18	0	2	0	2	0.0013
Pongo	946	1.17	8.43	12.59	17.49	0	25	0	25	0.0275
Gorilla	3486	1.98	13.05	20.96	33.34	2	317	12	331	0.0952

[a] ***np*** = number of pairwise comparisons; c_{ff} = number of female-female distances ≥ distance between fossils; c_{mf} = number of male-female distances ≥ distance between fossils; c_{mm} = number of male-male distances ≥ distance between fossils; ***c*** = total number of pairwise distances between individuals ≥ distance between fossils.

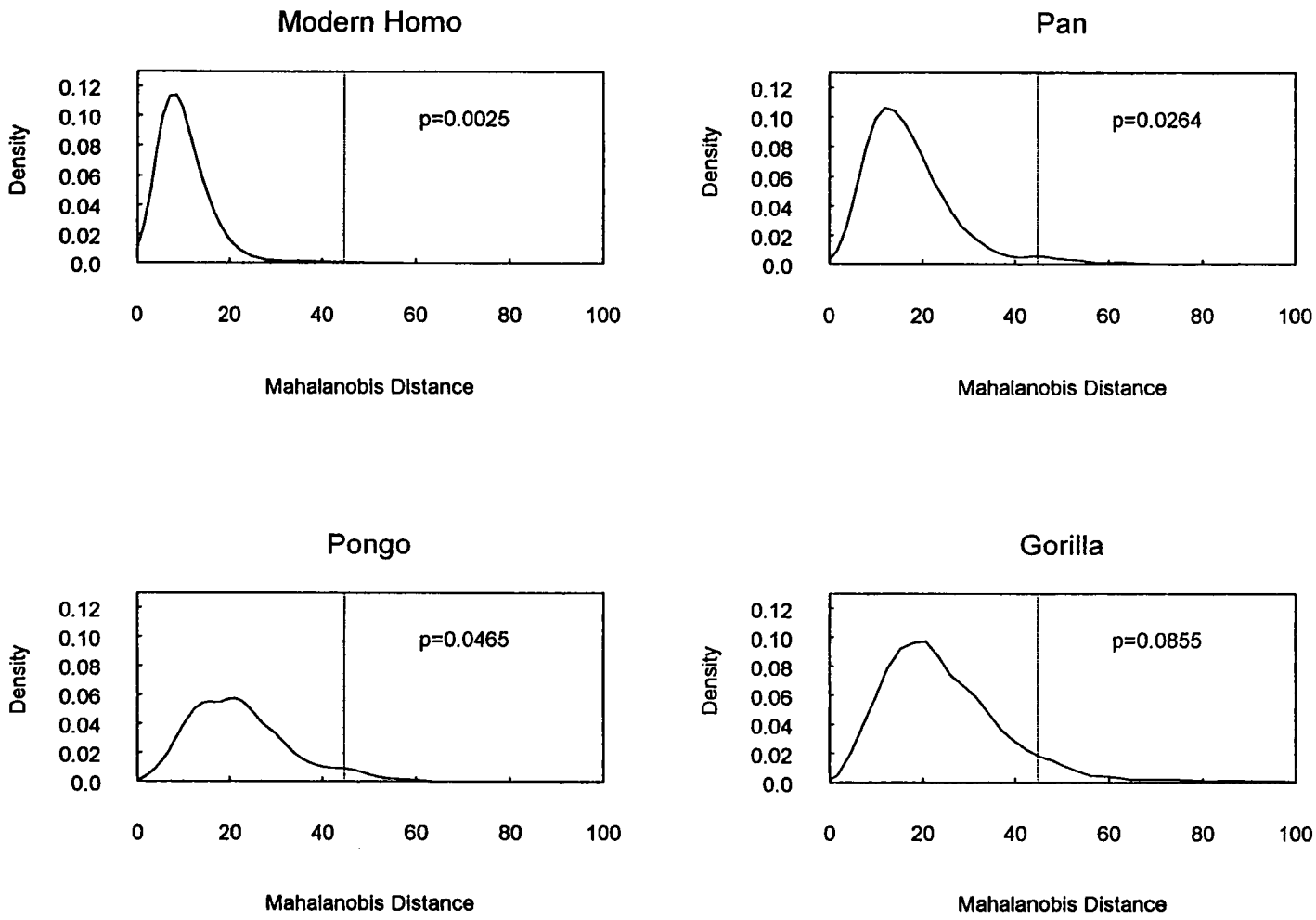


Figure 11. The smoothed distributions of all possible Mahalanobis distances between individuals in the reference samples plotted against the Mahalanobis distance between KNM-ER 1470 and KNM-ER 1805. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

distances are as large or larger than that between KNM-ER 1470 and 1805 ($p = 0.0264$). When compared to the more sexually dimorphic species the distance between the fossils does not appear to be as extreme but it is still relatively large. It is approximately equal to the 95th percentile of the orangutan distribution where 43 of the 946 distances equal or exceed the fossil distance ($p = 0.047$). In the *Gorilla* sample there are 3486 pairwise distances, 297 of these match or surpass the distance between KNM-ER 1470 and 1805 ($p = 0.0855$).

The results presented in Table 31 suggest that if KNM-ER 1470 and 1805 are conspecific the differences between them most likely reflect sexual dimorphism, although it is also possible that they are of the same sex. In all of the pongid reference samples more than 60% of the pairwise distances that are equal to or greater than the D^2 between the fossils are between males and females. In the modern human sample 50% (5) of these distances are between males and females and 50% are between females.

In Figure 12 the distributions of all possible shape distances between individuals in the *Pan*, *Pongo*, *Gorilla* and modern human sample are shown. Overall, the results of the comparisons of the shape distances presented in Table 31 and Figure 12 are similar to the comparisons of the Mahalanobis distances, although the shape differences between KNM-ER 1470 and 1805 are not quite as extreme. The shape D^2 between the fossils is 34.21. In the modern human distribution only 43 of the 4371 pairwise distances exceed or equal this distance ($p = 0.0101$). In the chimpanzee distribution 108 out of 2346 distances are equal to or greater than the shape distance between the fossils ($p = 0.0465$). For the orangutan sample 80 out of 946 distances and for the gorilla sample 41 out of 3486 pairwise distances are greater than or equal to the shape distance between KNM-ER 1470 and 1805 ($p = 0.0856$ for *Pongo* and 0.1196 for *Gorilla*). Thus the probability of randomly sampling two individuals which are as different in shape as KNM-ER 1470 and 1805 from a species as dimorphic as modern humans is small. If that species were as dimorphic as chimpanzees

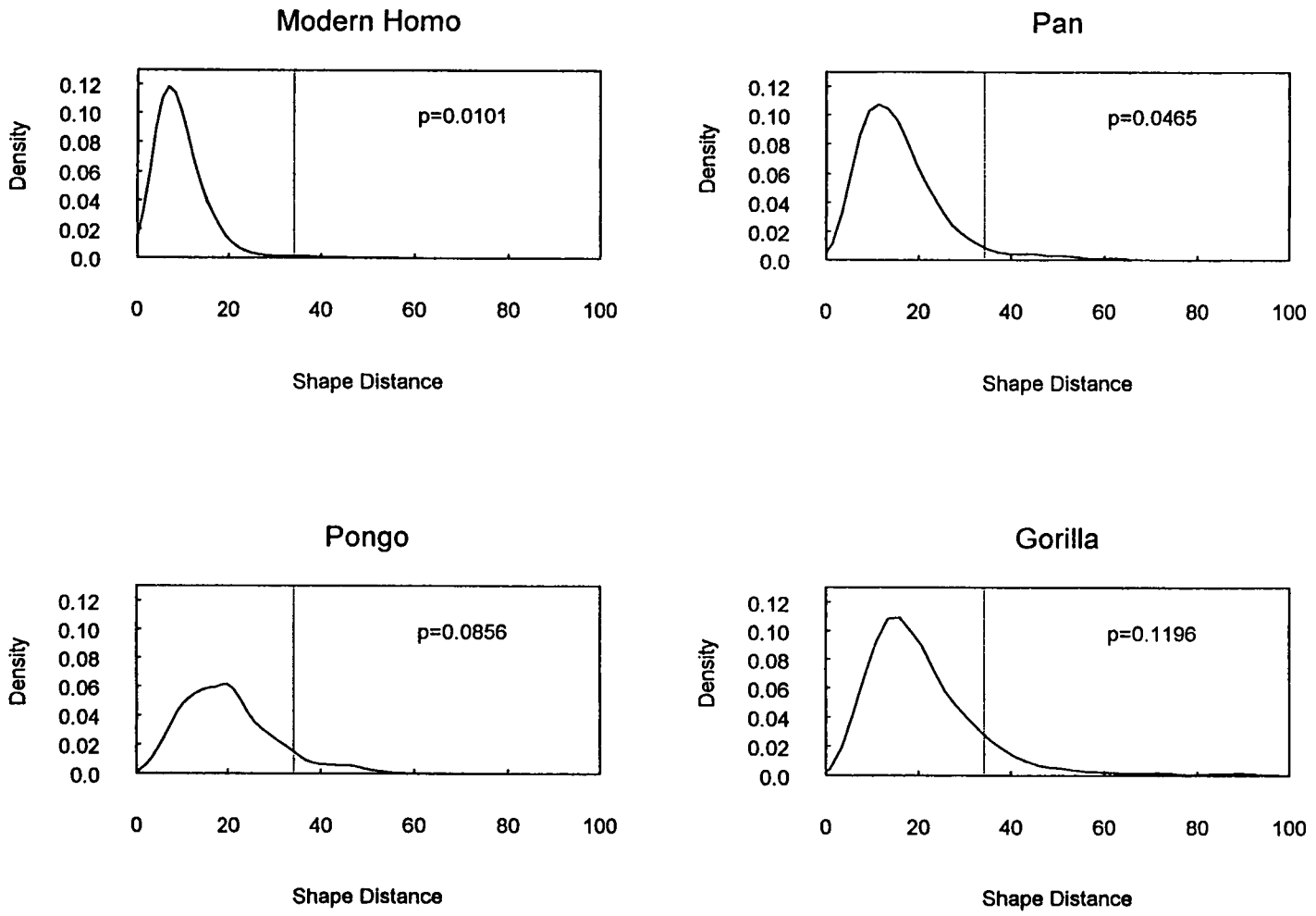


Figure 12. The smoothed distributions of all possible shape distances between individuals in the reference samples plotted against the shape distance between KNM-ER 1470 and KNM-ER 1805. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

this probability is somewhat larger and if it were as dimorphic as orangutans or gorillas it is even larger, but even for these species the probability of finding two individuals as disparate as KNM-ER 1470 and 1805 is not particularly large.

The results for the shape comparisons given in Table 31 suggest that if KNM-ER 1470 and 1805 do belong to the same species the shape differences between them could be found between individuals of the same or opposite sex, although it may be more likely that the shape differences between them reflect sexual dimorphism. In all of the reference samples more than 50% of the shape distances that are equal to or greater than the shape distance between the fossils are between males and females. In the modern human sample 58% (25 out of 43) of the distances as large as, or larger than, the distance between the fossils are between males and females. For the pongids 63% (68 out of 108) of the chimpanzee, 61% (49 out of 80) of the orangutan and 54% (224 out of 416) of the gorilla pairwise distances that exceed the shape D^2 between KNM-ER 1470 and 1805 are between males and females. In the modern humans none of the shape distances between males is greater than the distance between the fossils, but in the three pongid samples this distance is equalled or exceeded by distances between males and males and between females and females.

The distributions of size distances for the modern hominoids are shown in Figure 13, and here it is apparent that in terms of size KNM-ER 1470 and 1805 are quite different from one another. The results in Table 31 show that the size distance between the fossils of 10.54 is large when compared to the size distances seen in all of the extant hominoid samples. The size distance between the fossils exceeds the maximum size distance in the modern human sample (7.04), and consequently the probability of finding a size difference as large as or larger than the distance between KNM-ER 1470 and 1805 in a species as dimorphic as modern humans is very small ($p=0.0002$). The distance between the fossils does fall within the range of distances seen in the pongids, but the probability of seeing such a

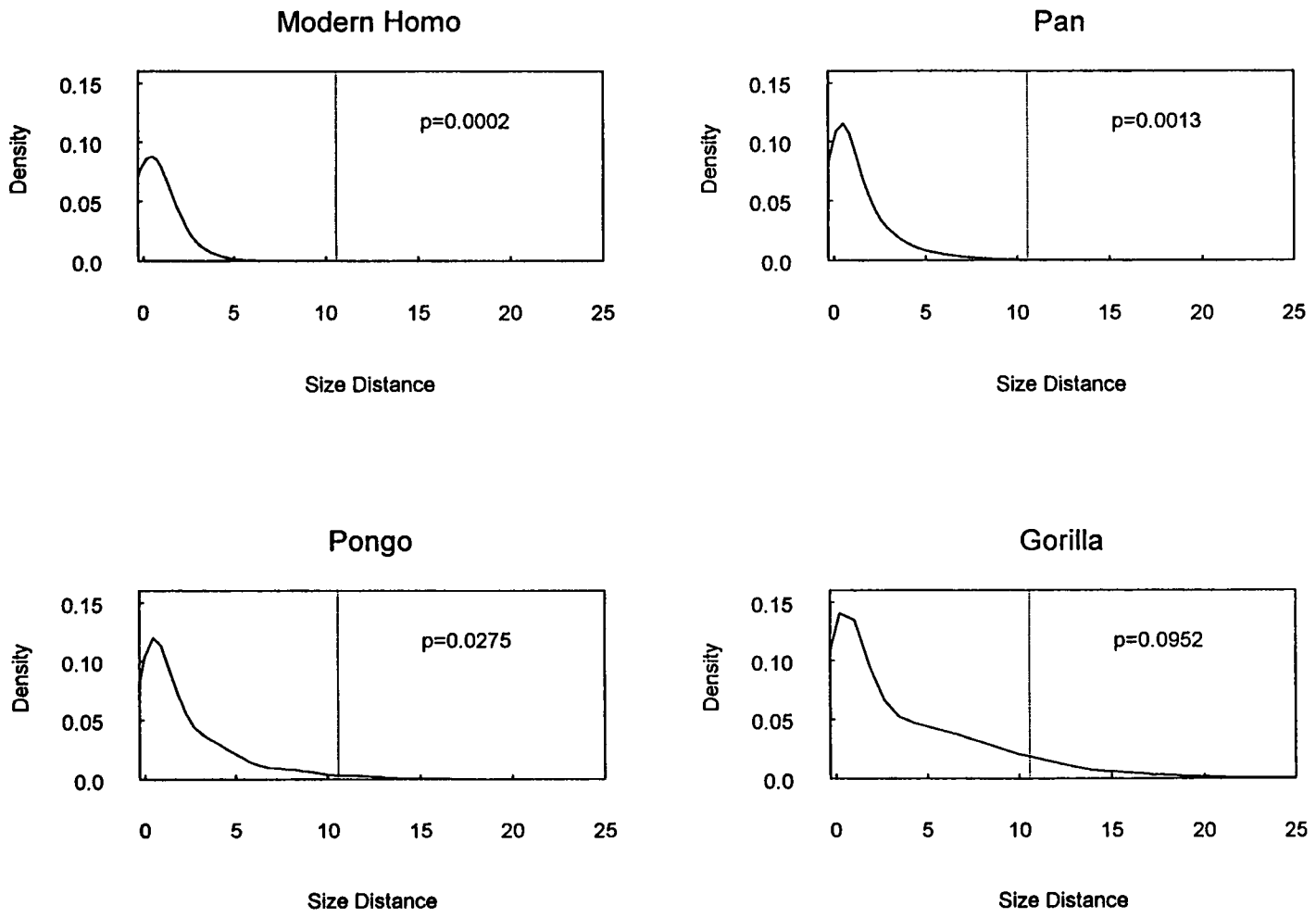


Figure 13. The smoothed distributions of all possible size distances between individuals in the reference samples plotted against the size distance between KNM-ER 1470 and KNM-ER 1805. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

distance in these species is relatively small, even for the very dimorphic gorillas. In the *Pan* reference sample only 2 out of 2346 pairwise distances are equal to or greater than the distance between KNM-ER 1470 and 1805 ($p=0.0013$); in the orangutans sample 25 of the 946 distances between pairs of individuals match or exceed the distance between the fossils ($p=0.0275$) and in the gorilla sample 331 out of 3486 pairwise distances exceed or equal the size distance between KNM-ER 1470 and 1805 ($p=0.0952$).

If KNM-ER 1470 and 1805 are derived from a species as dimorphic as *Pan*, *Pongo* or *Gorilla* the results in Table 31 indicate that they are almost certainly male and female. For the chimpanzees and orangutans all of the size distances that exceed the distance between the fossils are between males and females and in the gorilla sample 96% (317 out of 331) of the size distances equal to or greater than the distance between KNM-ER 1470 and 1805 are between males and females.

Comparisons with Plio-Pleistocene hominids

The comparisons of the differences between KNM-ER 1470 and 1805 with the differences between other Plio-Pleistocene hominids are based on the same set of measurements as the comparisons with the modern hominoids. In addition to KNM-ER 1470 and 1805 the fossil hominid sample consists of 6 specimens. In this sample there are two pairs of individuals that are probably conspecific: KNM-ER 406 and 407, and KNM-ER 3733 and 3883.

The matrix of Mahalanobis distances between the fossils is given in Table 32 and for comparative purposes the descriptive statistics for the modern reference samples are presented in Table 33. As discussed above the Mahalanobis distance between KNM-ER 1470 and 1805 (44.74) is relatively large, especially when compared to the distances in the modern human sample, where it exceeds the upper 99th percentile, and the chimpanzee sample where it falls between the upper 95th and 99th percentiles, but even when compared to the more dimorphic orangutans and gorillas the distance between the fossils is relatively

Table 32. Mahalanobis distances among KNM-ER 1470, KNM-ER 1805, KNM-ER 1813 and other Plio-Pleistocene hominids based on nine calvarial measurements. Variables used: PAC, PAA, BSC, SPC, LAC, ASB, MFB, XPB and POB.

	ER 1805	ER 1813	ER 406	ER 407	Sts 5	ER 3733	ER 3883
ER 1470	44.74	45.83	51.18	55.08	51.42	22.89	20.52
ER 1805		61.50	98.08	74.17	80.66	74.96	77.90
ER 1813			75.31	26.98	35.60	72.93	98.75
ER 406				51.18	49.35	117.67	95.74
ER 407					50.57	119.86	128.21
Sts 5						70.48	73.95
ER 3733							9.62

Table 33. Descriptive statistics for all pairwise Mahalanobis distances within the modern reference species based on nine calvarial measurements. Variables used: PAC, PAA, BSC, SPC, LAC, ASB, MFB, XPB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance
Homo	4371	8.94	20.18	35.14	56.53
Pan	2346	15.24	35.51	52.11	89.92
Pongo	946	20.78	44.23	53.53	61.73
Gorilla	3486	22.20	50.87	86.13	123.45

large. The Mahalanobis D^2 between KNM-ER 1470 and 1805 is also much larger than the distance of 9.62 between KNM-ER 3733 and 3883, but considerably smaller than the distance of 51.18 between the male and female *A. boisei* specimens, KNM-ER 406 and 407. The Mahalanobis D^2 between KNM-ER 1470 and 1805 is also not as large as the distances between fossils that represent different species. The smallest D^2 between representatives of different species is the distance between KNM-ER 406 and Sts 5 (49.35) and the largest is between KNM-ER 407 and KNM-ER 3883 (128.21). The distances between fossil hominids that are not conspecific equal or exceed the distances at the upper 95th percentile for all of the modern reference groups, and the distances between the *Homo erectus* and *A. africanus*, and between the *Homo erectus* and *A. boisei* crania exceed the upper 99th percentiles for the modern human, chimpanzee and orangutan samples.

The matrix of shape distances between the Plio-Pleistocene hominids is shown in Table 34 and the descriptive statistics for the pairwise shape distances within the modern reference species are given in Table 35. The shape D^2 between KNM-ER 1470 and 1805 is 34.21. When compared to the modern hominoids this distance is relatively large, even in the very dimorphic gorilla sample the probability of equalling or exceeding the distance between the fossils is only 0.12 (Table 31). A comparison of the shape distance between KNM-ER 1470 and 1805 with the shape distances between other Plio-Pleistocene hominids yields results that are very similar to the comparisons of the Mahalanobis distances. The shape distance of 34.21 between KNM-ER 1470 and 1805 is much larger than the shape D^2 between the two *Homo erectus* crania, KNM-ER 3733 and 3883 (9.44) but it is considerably smaller than the distance of 50.26 between KNM-ER 406 and 407. The distance between KNM-ER 1470 and 1805 is also smaller than all of the shape distances between fossil hominids that are not conspecific. The largest shape distance between representatives of different species is the D^2 between KNM-ER 407 and KNM-ER 3883 (117.41) and the smallest is the distance between KNM-ER 406 and Sts 5 (47.60). All of the distances

Table 34. Shape distances among KNM-ER 1470, KNM-ER 1805, KNM-ER 1813 and other Plio-Pleistocene hominids based on nine calvarial measurements. Variables used: PAC, PAA, BSC, SPC, LAC, ASB, MFB, XPB and POB.

	ER 1805	ER 1813	ER 406	ER 407	Sts 5	ER 3733	ER 3883
ER 1470	34.21	33.20	47.96	47.50	41.70	22.88	20.24
ER 1805		61.41	95.97	73.93	80.65	63.74	63.63
ER 1813			72.21	26.34	35.41	59.55	82.06
ER 406				50.26	47.60	114.07	90.33
ER 407					50.44	111.69	117.41
Sts 5						60.10	60.64
ER 3733							9.44

Table 35. Descriptive statistics for all pairwise shape distances within the modern reference species based on nine calvarial measurements. Variables used: PAC, PAA, BSC, SPC, LAC, ASB, MFB, XPB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance
Homo	4371	8.23	19.13	33.17	56.44
Pan	2346	14.07	33.34	51.76	87.28
Pongo	946	18.84	40.06	48.97	58.82
Gorilla	3486	18.40	44.89	83.25	111.81

between fossils that represent different species are above the upper 95th percentiles for all of the modern hominoids and nearly as large as, or larger than, the upper 99th percentiles for the modern *Homo*, *Pan* and *Pongo* samples.

The large size disparity between KNM-ER 1470 and 1805 seen in the comparisons with the modern hominoids is also evident in the comparisons with the fossil hominids. Table 36 shows the matrix of size only distances between the Plio-Pleistocene hominids, and in Table 37 the descriptive statistics for the pairwise size distances in the extant reference groups are given. The size distance between KNM-ER 1470 and 1805 is 10.54. This is much larger than the distances between conspecific hominids. The size distance between KNM-ER 406 and 407 is only 0.92, and the distance between KNM-ER 3733 and 3883 of 0.18 is even smaller. The size distance between KNM-ER 1470 and 1805 is also greater than, or approximately equal to, all but one of the distances between hominids that represent different species. Only the size distance between Sts 5 and KNM-ER 3883 (13.31) is larger than the size distance between KNM-ER 1470 and 1805. The size distance between these two crania is approximately equal to the distance of 10.79 between the female *A. boisei*, KNM-ER 407, and the *Homo erectus* calvarium KNM-ER 3883, and it is also approximately equal to the size distance between the gracile australopithecine Sts 5 and KNM-ER 3733.

In Figure 14 the positions of the fossils along the single size dimension are shown. Here it is easier to see how the size differences between KNM-ER 1470 and 1805 compares with the size differences between other fossil hominids. The size difference between KNM-ER 1470 and 1805 is much larger than the differences between KNM-ER 3733 and 3883, or between KNM-ER 406 and 407. It is also larger, in some cases much larger, than most of the size differences between fossils that represent different species. Only the size distance between Sts 5 and KNM-ER 3883 is appreciably larger. Note also that the size disparity between KNM-ER 1470 and 1813 is even greater than the difference between KNM-ER 1470 and 1805.

Table 36. Size distances among KNM-ER 1470, KNM-ER 1805, KNM-ER 1813 and other Plio-Pleistocene hominids based on nine calvarial measurements. Variables used: PAC, PAA, BSC, SPC, LAC, ASB, MFB, XPB and POB.

	ER 1805	ER 1813	ER 406	ER 407	Sts 5	ER 3733	ER 3883
ER 1470	10.54	12.63	3.22	7.58	9.71	0.01	0.28
ER 1805		0.09	2.11	0.24	0.02	11.22	14.27
ER 1813			3.10	0.64	0.19	13.38	16.69
ER 406				0.92	1.75	3.60	5.41
ER 407					0.13	8.17	10.79
Sts 5						10.37	13.31
ER 3733							0.18

Table 37. Descriptive statistics for all pairwise size distances within the modern reference species based on nine calvarial measurements. Variables used: PAC, PAA, BSC, SPC, LAC, ASB, MFB, XPB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance
Homo	4371	0.35	2.55	3.94	7.04
Pan	2346	0.64	4.82	7.68	12.18
Pongo	946	1.17	8.43	12.59	17.49
Gorilla	3486	1.98	13.05	20.96	33.34

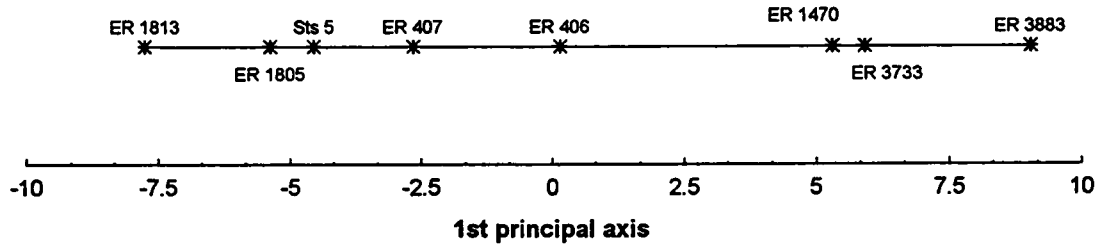


Figure 14. Size differences among KNM-ER 1470, KNM-ER 1813, KNM-ER 1805 and other Plio-Pleistocene hominids.

KNM-ER 1470 and OH 24

The magnitude and pattern of variation in the vault

Comparisons with modern hominoids

For the calvarium the multivariate comparisons of the differences between KNM-ER 1470 and OH 24 and between individuals in the extant hominoid samples are based on 9 variables: GOL, GBC, MFB, PAC, PAA, BSC, ASB and POB. The results of these comparisons are given in Table 38.

In Figure 15 the distributions of Mahalanobis distances between pairs of individuals are shown for each reference group. The results presented in Table 38 and Figure 15 show that in the vault the differences between KNM-ER 1470 and OH 24 are not as dramatic as the differences between KNM-ER 1470 and 1813 or between KNM-ER 1470 and 1805. The Mahalanobis D^2 between the fossils is 24.79. This is larger than the median D^2s but below the 95th percentiles for all four reference groups. For the modern human sample there are 4371 possible pairwise distances between individuals, 304 of which are equal to or greater

TABLE 38. Descriptive statistics and results[a] of the multivariate distance comparisons based on calvarial measurements: KNM-ER 1470 - OH 24. Variables used: GOL, GBC, GBA, MFB, PAC, PAA, BSC, ASB and POB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance	c_{ff}	c_{mf}	c_{mm}	c	p
Mahalanobis Distances - distance between KNM-ER 1470 and OH 24 = 24.79										
Homo	4371	9.21	41.11	104.35	138.02	143	157	4	304	0.0698
Pan	2346	14.00	36.23	51.70	95.08	89	186	76	351	0.1500
Pongo	946	19.43	37.18	46.46	51.29	66	175	33	274	0.2907
Gorilla	3486	19.96	46.41	83.82	115.36	174	800	219	1193	0.3425
Shape Distances - distance between KNM-ER 1470 and OH 24 = 21.02										
Homo	4371	8.50	38.63	103.08	137.44	157	176	15	348	0.0798
Pan	2346	12.67	34.32	50.86	94.50	112	216	101	429	0.1833
Pongo	946	17.26	35.29	43.22	50.65	96	186	44	326	0.3457
Gorilla	3486	15.97	38.91	80.68	105.69	235	614	265	1114	0.3198
Size Distances - distance between KNM-ER 1470 and OH 24 = 3.77										
Homo	4371	0.36	2.67	4.55	7.18	0	82	0	82	0.0190
Pan	2346	0.69	4.96	7.44	10.12	41	141	29	211	0.0904
Pongo	946	0.99	7.20	11.46	17.43	17	151	4	172	0.1829
Gorilla	3486	2.19	13.51	21.05	37.57	56	1239	99	1394	0.4002

[a] np = number of pairwise comparisons; c_{ff} = number of female-female distances ≥ distance between fossils; c_{mf} = number of male-female distances ≥ distance between fossils; c_{mm} = number of male-male distances ≥ distance between fossils; c = total number of pairwise distances between individuals ≥ distance between fossils.

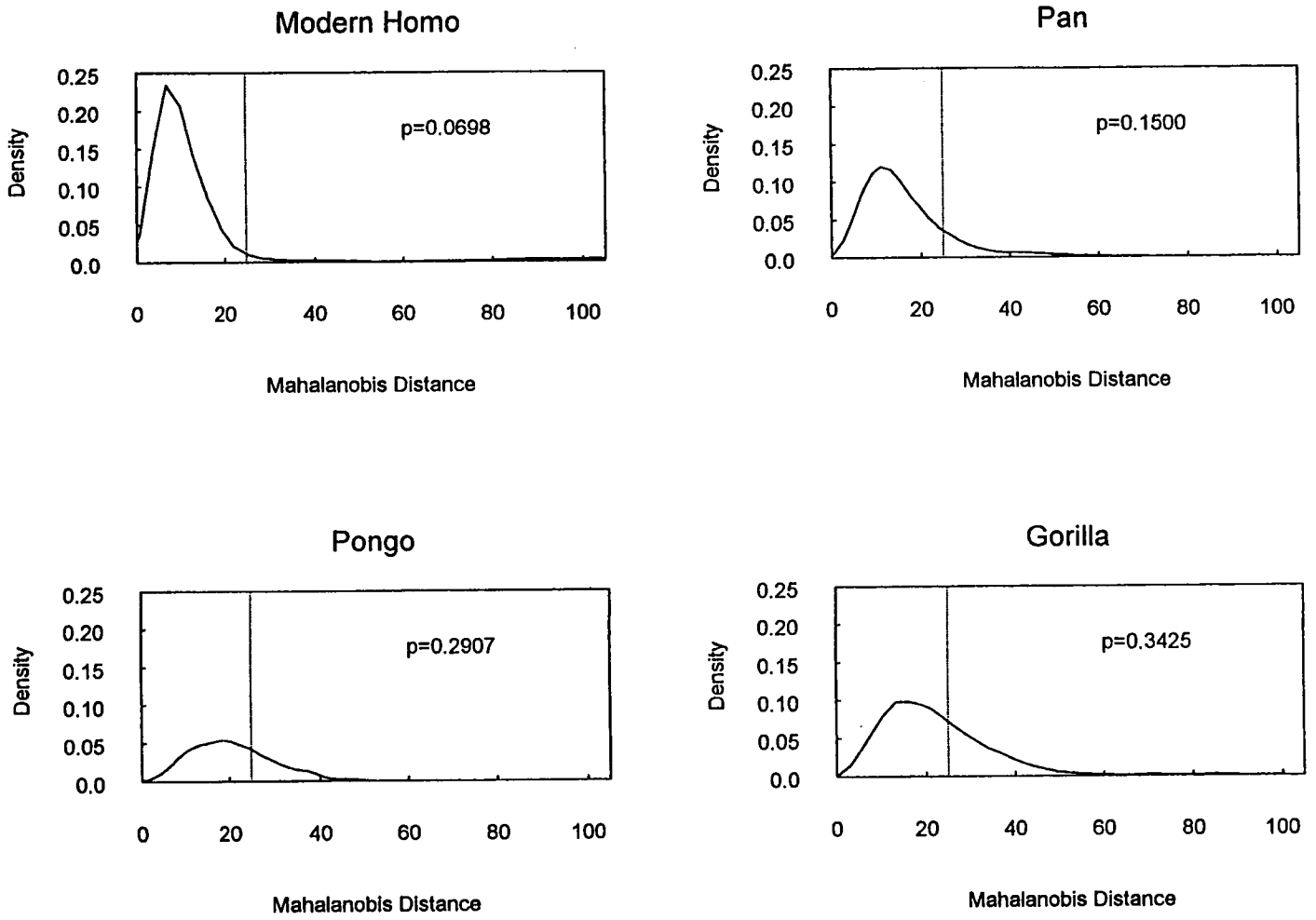


Figure 15. The smoothed distributions of all possible Mahalanobis distances between individuals in the reference samples plotted against the Mahalanobis distance between KNM-ER 1470 and OH 24 for the vault. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

than the Mahalanobis D^2 between KNM-ER 1470 and OH 24, and if the fossils represent a single species as sexually dimorphic as modern humans the probability of matching or exceeding the distance between them is 0.0698. In the chimpanzee sample an even larger proportion of the distances, 351 out of 2346, exceed the distance between KNM-ER 1470 and OH 24 ($p = 0.1502$). For the more dimorphic apes, *Pongo* and *Gorilla*, the probability of exceeding the distance between the fossils is even higher. In the orangutan sample 274 of the 946 possible distances between individuals are equal to or greater than the distance between KNM-ER 1470 and OH 24 ($p = 0.2907$) and in the gorilla sample 1193 out of 3486 distances exceed or equal this distance ($p = 0.3425$).

The results presented in Table 38 show that the overall differences between KNM-ER 1470 and OH 24, as measured by the Mahalanobis distance between them, need not be due to sexual dimorphism. In all of the reference samples the Mahalanobis D^2 between the fossils is equalled or exceeded by distances between males and females and between individuals of the same sex. In the more sexually dimorphic species, *Pongo* and *Gorilla*, a larger proportion of these differences (64% for *Pongo* and 67% for *Gorilla*) are between males and females than in the less dimorphic species. Fifty-three percent of distances in the chimpanzee sample and 51% of the distances in the modern human sample that are equal to or greater than the distance between KNM-ER 1470 and OH 24 are between males and females. Thus, if KNM-ER 1470 and OH 24 represent a single species that is as dimorphic as modern humans or chimpanzees the two fossils could be of the same or opposite sex, but if they are derived from a species as dimorphic as *Pongo* or *Gorilla* they are more likely to be male and female, although the probability that they are of the same sex is still relatively large.

With respect to the shape of the vault the differences between KNM-ER 1470 and OH 24 also do not appear to be unusually large, except perhaps when compared to the modern humans. The distributions of pairwise shape D^2s within the four reference samples are

shown in Figure 16. Here it is evident that in the pongids the probability of finding two individuals that are separated by a shape distance greater than the distance between KNM-ER 1470 and OH 24 is relatively large. The shape D^2 between KNM-ER 1470 and OH 24 is 21.02. This is larger than the median distances but below the upper 95th percentiles for all of the reference samples (Table 38). In the modern human sample 348 of the 4371 possible pairwise shape distances exceed or equal the distance between the fossils ($p = 0.0798$). In the pongid samples an even larger proportion of pairwise shape distances exceed the D^2 between KNM-ER 1470 and OH 24. For *Pan* 429 out of 2346, for *Pongo* 326 out of 946 and for *Gorilla* 1114 out of 3486 pairwise distances are equal to or greater than the shape distance between the fossils ($p = 0.1833$ for *Pan*, 0.3457 for *Pongo* and 0.3198 for *Gorilla*).

The results presented in Table 38 demonstrate that the shape differences between KNM-ER 1470 and OH 24 could be found between individuals of the same or opposite sex. In the modern human and chimpanzee samples 50% (176 out of 348 for modern humans and 216 out of 429 for *Pan*) of the shape distances that exceed or equal the fossils' shape distance are between males and females. In the orangutan sample 57% (186 out of 326) of the shape D^2s that are equal to or greater than the distance between KNM-ER 1470 and OH 24 are between males and females, and in the gorilla sample this proportion is 55% (614 out of 1114).

For the vault the size distance between KNM-ER 1470 and OH 24 is 3.77. When this distance is compared with the distributions of pairwise size distances for the reference samples (Figure 17, Table 38) it is apparent that it is large relative to the distances seen between modern humans, but in the pongid samples, particularly the orangutan and gorilla samples, a large proportion of the distances between individuals exceed the distance between KNM-ER 1470 and OH 24. For the modern human sample 82 of the 4371 distances between individuals are equal to or greater than the fossils' size distance

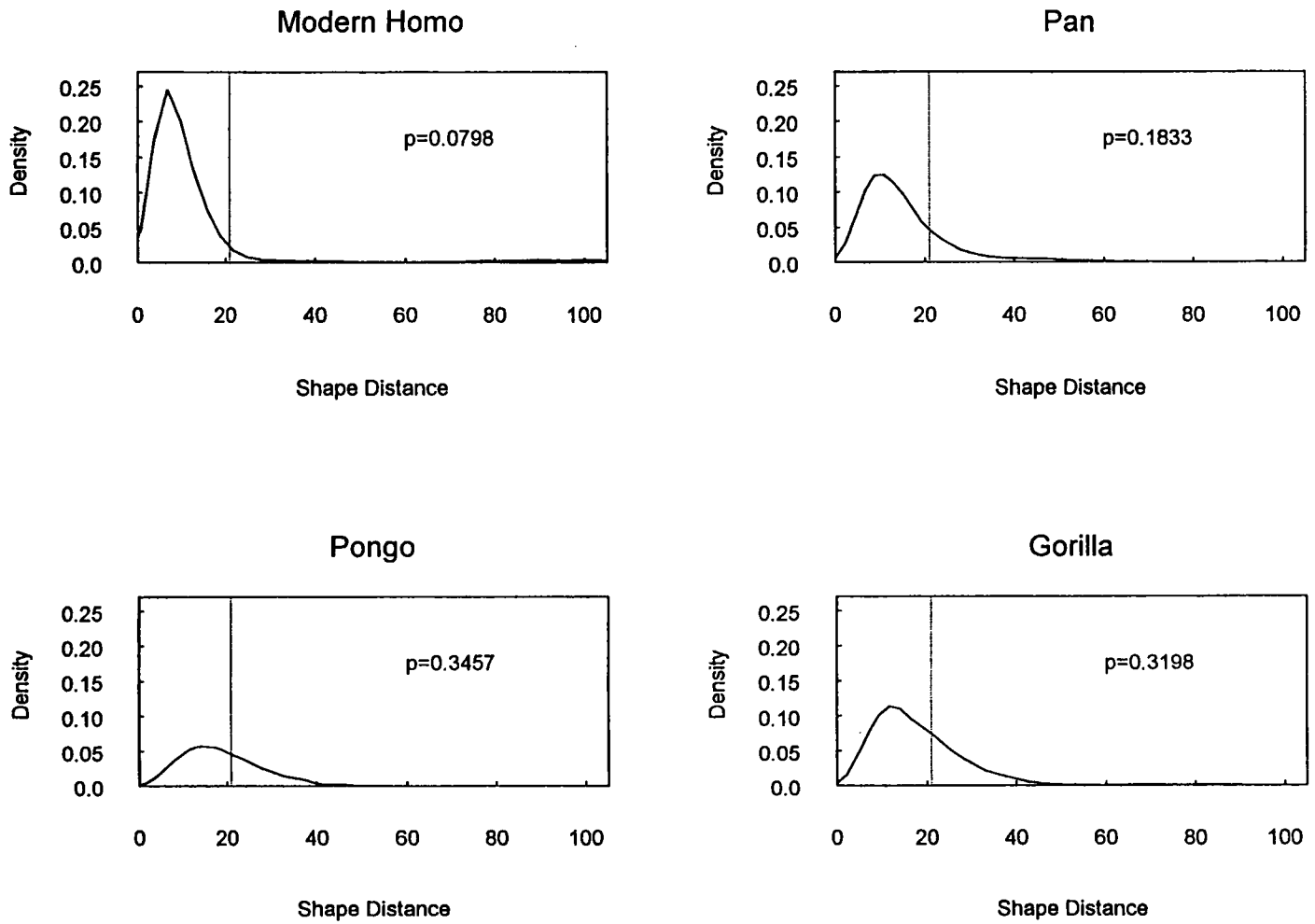


Figure 16. The smoothed distributions of all possible shape distances between individuals in the reference samples plotted against the shape distance between KNM-ER 1470 and OH 24 for the vault. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

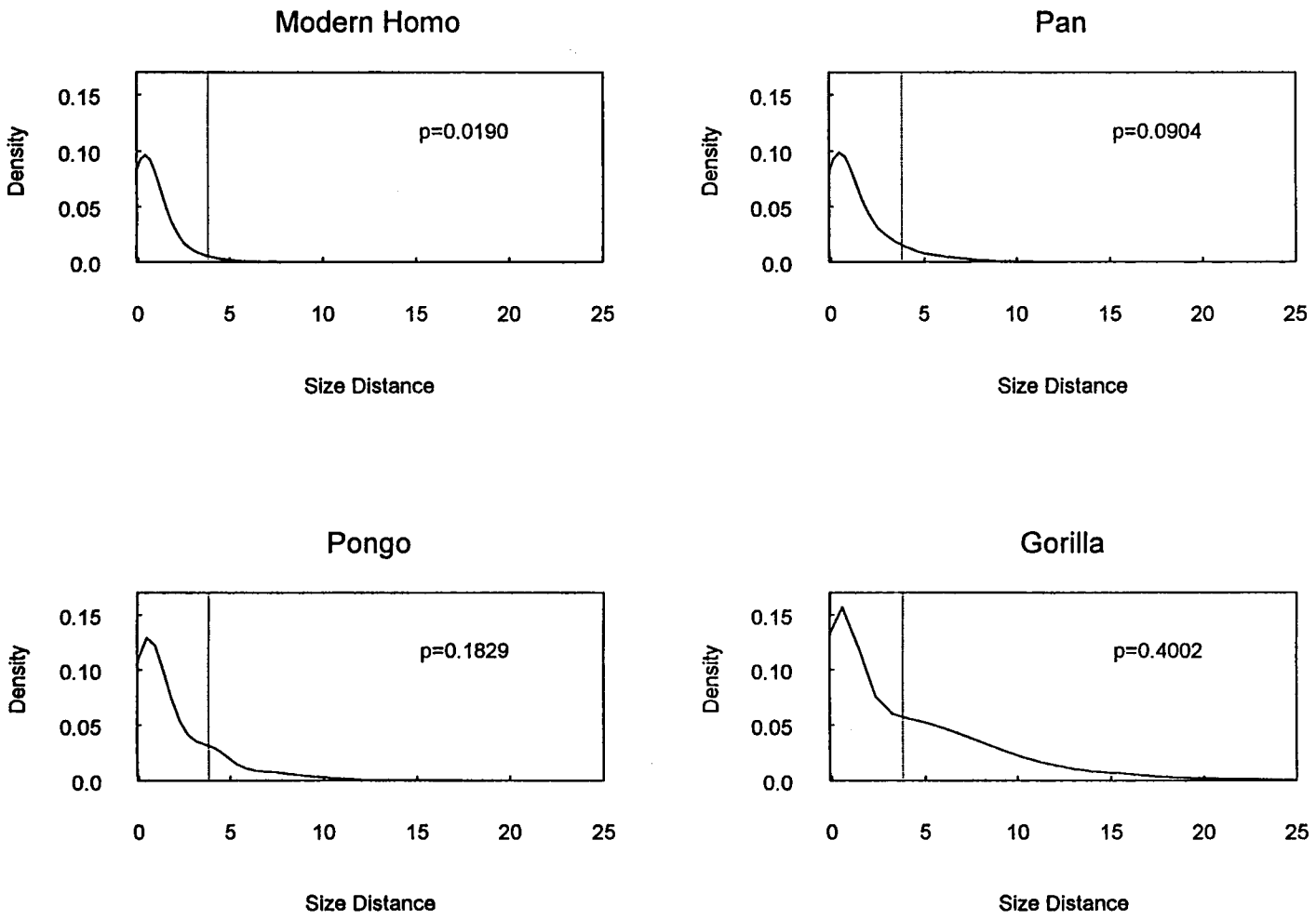


Figure 17. The smoothed distributions of all possible size distances between individuals in the reference samples plotted against the size distance between KNM-ER 1470 and OH 24 for the vault. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

($p = 0.0190$). In the chimpanzee reference group 211 out of 2346 pairwise distances match or surpass the distance between the fossils ($p = 0.0904$) and in the orangutan and gorilla samples 172 out of 946, and 1394 out of 3486 distances, respectively, are as large as or larger than the size between KNM-ER 1470 and OH 24 ($p = 0.1829$ for *Pongo* and 0.4002 for *Gorilla*).

If KNM-ER 1470 and OH 24 are conspecific the results shown in Table 38 strongly suggest that the size differences between them are due to sexual dimorphism. For the modern humans all of the size distances that are greater than or equal to the size distance between the fossils are between males and females. Sixty-nine percent (141 out of 211) of the size distances between chimpanzees that are larger or equal to the distance between KNM-ER 1470 and OH 24 are between males and females, and for the orangutan and gorilla samples 87% (151 out of 172) and 89% (1239 out of 1394) of the distances that equal or surpass the size distance between the fossils are between males and females.

Comparisons with Plio-Pleistocene hominids

The comparisons of the differences between KNM-ER 1470 and OH 24 with the differences between other Plio-Pleistocene hominids are based on the same 8 measurements (GBC, GBA, PAC, PAA, BSC, ASB, MFB and POB) and the same fossil hominids used in the comparisons of KNM-ER 1470 and 1813. In the comparative group there are three pairs of fossils that are most likely conspecific: KNM-ER 3733 and 3883 (*Homo erectus*), KNM-ER 406 and 407 (*A. boisei*) and Sts 5 and 71 (*A. africanus*).

The matrix of Mahalanobis distances between the fossils is shown in Table 18 (p. 185), and for comparative purposes the descriptive statistics for the distances within the modern reference groups are presented in Table 19. The distance between KNM-ER 1470 and OH 24 of 17.98 is above the median distances, but below the upper 95th percentiles of the modern human and chimpanzee samples, and it is very close to the median distances of the orangutan and gorilla samples. Compared to the modern reference groups the distance

between KNM-ER 1470 and OH 24 does not appear to be unusually large, and this is also true when it is compared to the distances between other hominids. The observed D^2 of 17.98 between KNM-ER 1470 and OH 24 is smaller than the distances between KNM-ER 406 and 407 (22.05), between Sts 5 and 71 (30.88) and between KNM-ER 3733 and 3883 (23.12). With the exception of the distance between KNM-ER 407 and Sts 5 it is also considerably smaller than the distances between fossils that are not conspecific. The distance between the female *A. boisei* cranium KNM-ER 407 and the gracile australopithecine Sts 5 is 13.00. The next smallest distance between representatives of different species is the distance of 34.23 between KNM-ER 407 and Sts 71. This is nearly twice the distance between KNM-ER 1470 and OH 24. The largest distance between different species is the distance of 136.96 between KNM-ER 406 and 3733.

In Table 20 (p. 187) the matrix of shape only distances for the fossil hominids is shown and the descriptive statistics for the shape distances in the modern reference groups are given in Table 21. The results of these comparisons are very similar to the comparisons based on the Mahalanobis distances. The shape distance between KNM-ER 1470 and OH 24 (14.52) is larger than the median distances but below the upper 95th percentiles for modern *Homo* and *Pan* and it is close to the median shape distances in *Pongo* and *Gorilla*. The shape D^2 between KNM-ER 1470 and OH 24 is also smaller than the shape distances between conspecific fossils. The distance of 14.52 is less than the distance between KNM-ER 406 and 407 (20.32), between Sts 5 and 71(30.13) and between KNM-ER 3733 and 3883 (22.78). In addition, the shape distance between OH 24 and KNM-ER 1470 is much smaller than the distances between the *Homo erectus* and *A. africanus* specimens (43.58 - 83.80), between the *A. boisei* and *Homo erectus* vaults (49.28 - 135.48) and between KNM-ER 406 and Sts 5 and 71 (38.18 and 35.33). Only the distance of 12.98 between KNM-ER 407 and Sts 5 is smaller.

In Table 22 (p. 189) the matrix of size distances between fossil hominids is presented and the descriptive statistics for the size distances between individuals in the modern comparative samples are given in Table 23. When compared to the size differences between the other Plio-Pleistocene hominids the differences between KNM-ER 1470 and OH 24 are more pronounced than the overall or shape differences. The size distance between KNM-ER 1470 and OH 24 of 3.46 is larger than any of the size D^2s between conspecific hominids: the size distance between KNM-ER 3733 and 3883 is only 0.35; the distance between Sts 5 and 71 is 0.75; and the size distance between the male and female *A. boisei*, KNM-ER 406 and 407 is 1.74. The size distance between KNM-ER 1470 and OH 24 falls within the range of size distances between fossils that are not conspecific. It is much smaller than any of the distances between *A. africanus* and *Homo erectus* (7.04 - 16.87) and it is also smaller than the distances between KNM-ER 407 and KNM-ER 3733 or 3883 (6.43 and 9.77), but it is larger than the size distances between KNM-ER 406 and the two *Homo erectus* vaults (1.48 and 3.27).

The magnitude of the disparity between KNM-ER 1470 and OH 24 in the size of the vault can be seen more clearly in Figure 6 (p. 190). When the positions of the fossils along the single size dimension are shown it is apparent that the size difference between KNM-ER 1470 and OH 24 is larger than, but still comparable to, the size differences between conspecific hominids. It also appears to fall within the range of size distances between fossils that represent different species. For example, the size distance between KNM-ER 1470 and OH 24 is smaller than the distance between KNM-ER 3733 and Sts 5, but smaller than the distance between Sts 5 and KNM-ER 406 or 407.

The magnitude and pattern of variation in the face

Comparisons with modern hominoids

For the face the comparisons of KNM-ER 1470 and OH 24 with the modern hominoids are based on 11 measurements: EKB, OBB, OBH, IOB, NLB, NLH, NPH, MMH, MAB, PLB and CCB. The results of these comparisons are presented in Table 39.

The distributions of pairwise Mahalanobis distances within the reference samples are shown in Figure 18. The results in Table 39 and Figure 18 show that the differences between KNM-ER 1470 and OH 24 in the face are more pronounced than the differences in the vault. The Mahalanobis D^2 between the fossils is 42.12. This is considerably larger than the median distances for any of the reference groups and it is above the upper 99th percentile for modern *Homo*, but below the upper 95th percentiles for the three pongid samples. The distance between the fossils falls at the extreme upper end of the modern human distribution; only 6 out of the 3655 possible pairwise distances in this distribution are equal to or greater than 42.12 ($p=0.0019$). A larger proportion of pairwise D^2s in the chimpanzee sample equal or exceed the fossils' distance; in this sample 150 of the 2415 distances between individuals are as large as or larger than the distance between the fossils ($p=0.0625$). When compared to the more sexually dimorphic hominoids the differences between KNM-ER 1470 and OH 24 do not appear to be as pronounced. Out of 2016 pairwise distances between orangutans 199 ($p=0.0992$) are greater than or equal to the distance between the fossils, and in the gorilla sample 385 out of 3486 ($p=0.1107$) distances equal or exceed the D^2 between KNM-ER 1470 and OH 24. Thus, if the species *Homo habilis* were as dimorphic as modern humans the probability that KNM-ER 1470 and OH 24 both represent that species is very small. If *Homo habilis* were as dimorphic as *Pongo* or *Gorilla* this probability is considerably higher, but it is still relatively small.

If KNM-ER 1470 and OH 24 are conspecific the results presented in Table 39 indicate that the differences between them could be due in part to sexual dimorphism, or the two

TABLE 39. Descriptive statistics and results[a] of the multivariate distance comparisons based on facial measurements: KNM-ER 1470 - OH 24. Variables used: EKB, OBB, OBH, IOB, NLB, NLH, NPH, MMH, MAB, PLB, CCB.

reference species	*np*	median distance	upper 95th percentile	upper 99th percentile	maximum distance	c_{ff}	c_{mf}	c_{mm}	c	p
Mahalanobis Distances - distance between KNM-ER 1470 and OH 24 = 42.12										
Homo	3655	11.49	23.89	32.58	46.82	0	4	2	6	0.0019
Pan	2415	20.49	45.71	68.98	92.59	38	82	30	150	0.0625
Pongo	2016	25.65	47.31	56.79	64.11	28	134	37	199	0.0992
Gorilla	3486	25.19	59.63	236.02	396.03	64	230	91	385	0.1107
Shape Distances - distance between KNM-ER 1470 and OH 24 = 36.61										
Homo	3655	10.92	23.10	31.88	46.36	0	6	5	11	0.0033
Pan	2415	19.17	44.96	68.39	92.55	53	120	41	214	0.0890
Pongo	2016	21.55	42.51	53.44	62.61	49	130	55	234	0.1166
Gorilla	3486	22.14	56.84	232.11	389.07	83	211	125	419	0.1205
Size Distances - distance between KNM-ER 1470 and OH 24 = 5.51										
Homo	3655	0.29	2.13	3.31	5.81	0	2	0	2	0.0008
Pan	2415	0.52	4.00	6.42	10.39	12	21	8	41	0.0174
Pongo	2016	1.73	12.47	18.02	24.24	19	427	39	485	0.2411
Gorilla	3486	1.66	10.96	14.86	19.80	6	744	1	751	0.2157

[a] np = number of pairwise comparisons; c_{ff} = number of female-female distances ≥ distance between fossils; c_{mf} = number of male-female distances ≥ distance between fossils; c_{mm} = number of male-male distances ≥ distance between fossils; c = total number of pairwise distances between individuals ≥ distance between fossils.

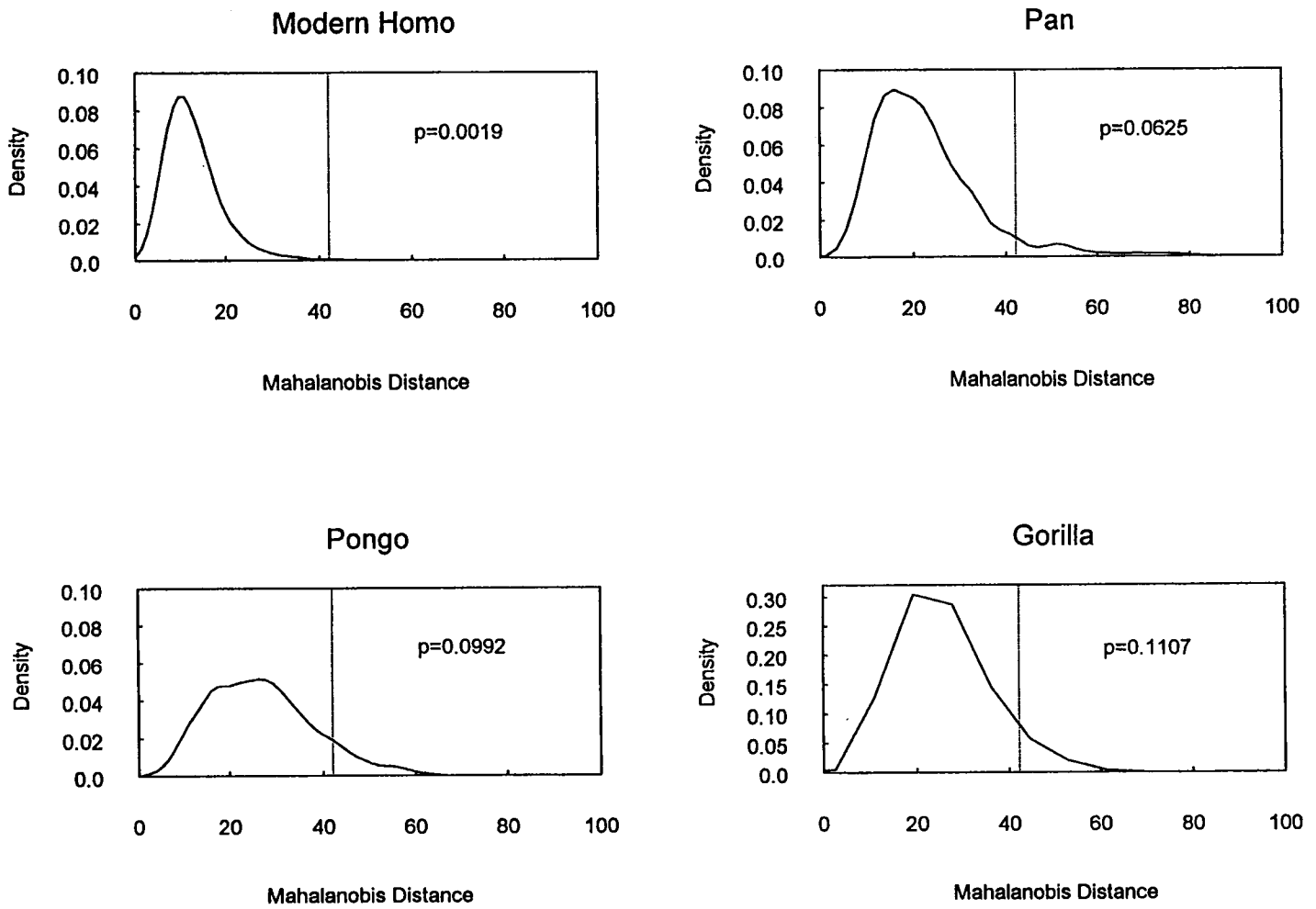


Figure 18. The smoothed distributions of all possible Mahalanobis distances between individuals in the reference samples plotted against the Mahalanobis distance between KNM-ER 1470 and OH 24 for the face. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

could be of the same sex, although this is somewhat less likely. In the modern human sample 67% (4 out of 6) of the Mahalanobis distances between individuals that are equal to or greater than the distance between KNM-ER 1470 and OH 24 are between males and females. In the chimpanzee sample 54% (82 out of 150) of the distances that are larger or equal to the distance between the fossils are between males and females. The proportion of male-female distances is larger for the orangutan and gorilla samples. Sixty-seven percent (134 out of 199) of the Mahalanobis distances in the orangutan sample, and 60% (230 out of 385) of the distances in the gorilla sample that equal or surpass the size distance between OH 24 and KNM-ER 1470 are between males and females.

Figure 19 shows the distributions of pairwise shape distances for the *Pan, Pongo, Gorilla* and modern *Homo* samples. Overall, the results presented in Table 39 and Figure 19 for the shape distances are similar to the results for the Mahalanobis distances. The shape distance of 36.61 between KNM-ER 1470 and OH 24 is very large relative to modern *Homo*, but it is not as extreme when compared to the pongid samples. In the modern human sample only 11 of 3655 pairwise shape distances between individuals are greater than or equal to the shape D^2 between KNM-ER 1470 and OH 24 ($p = 0.0033$). The probability of exceeding this distance is larger in the pongids. In the chimpanzee sample 214 out of 2415 pairwise shape distances are larger than, or as large as, the distance between the fossils ($p = 0.0625$). For the orangutans 234 out of 2016, and for the gorillas 419 out of 3486 pairwise distances are greater than or equal to the distance between KNM-ER 1470 and OH 24 ($p = 0.1166$ for *Pongo* and 0.1205 for *Gorilla*).

If OH 24 and KNM-ER 1470 do belong to the same species the results shown in Table 39 show that the shape differences between them could be seen between individuals of the same or opposite sex. The proportion of distances within the reference samples that are equal to or greater than the fossils' distance is between 51 and 56%. In the modern human and orangutan samples 55% (6 out of 11 for modern *Homo* and 130 out 234 for *Pongo*) of

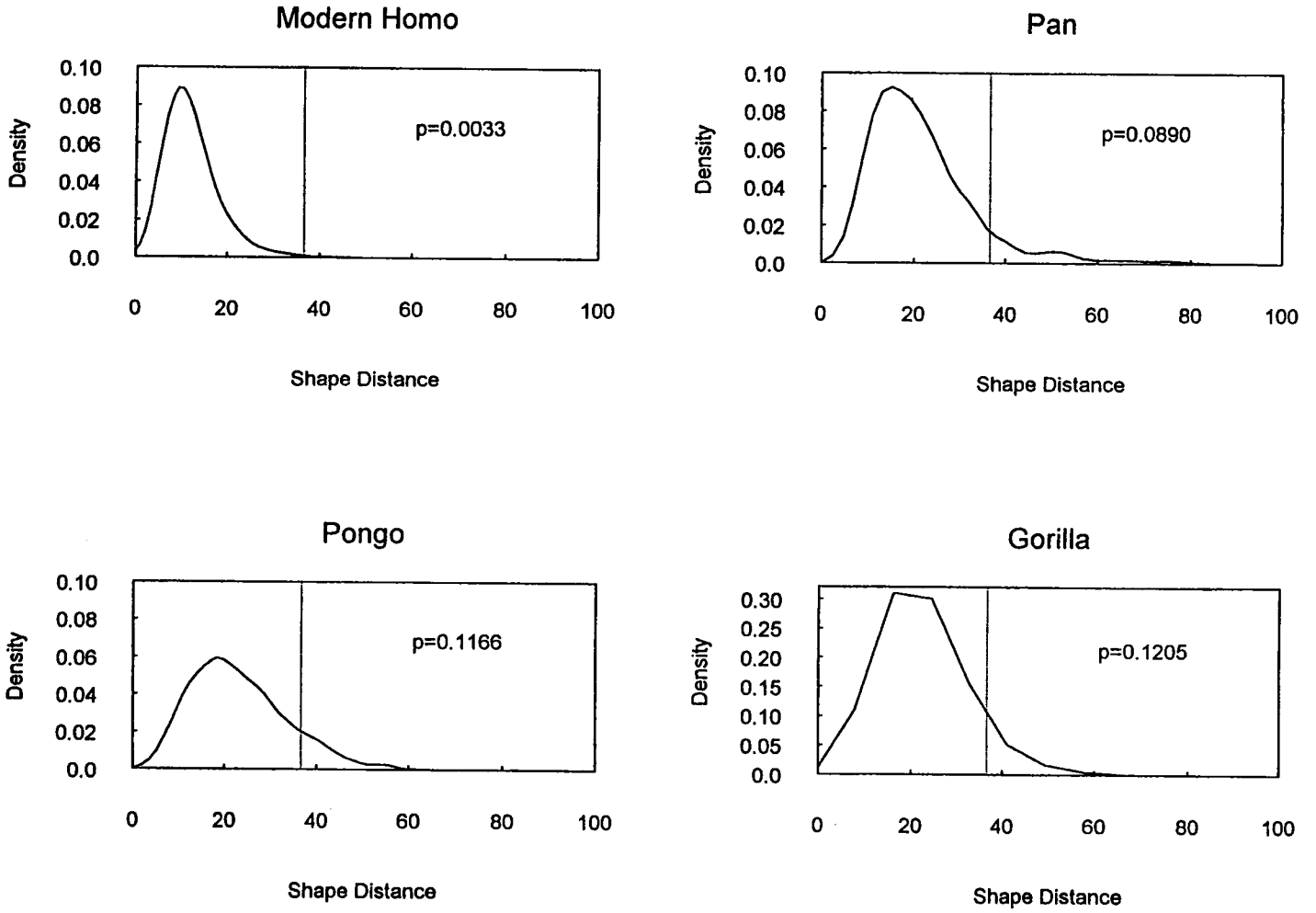


Figure 19. The smoothed distributions of all possible shape distances between individuals in the reference samples plotted against the shape distance between KNM-ER 1470 and OH 24 for the face. The vertical line shows the position of the distance between the fossils. *p* is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

the distances that match or surpass the distance between the fossils are between males and females. For the chimpanzees 56% (120 out of 214) and for the gorillas 51% (211 out of 419) of the shape distances that are equal to or greater than the distance between KNM-ER 1470 and OH 24 are between males and females.

The distributions of pairwise size distances for the reference samples are shown in Figure 20. Here it is apparent that there is a dichotomy in how the size difference between KNM-ER 1470 and OH 24 compares with the size differences seen in the modern hominoids. The size distance between the fossils is large relative to the less sexually dimorphic species, *Pan* and modern *Homo*, but it is not unusually large when compared to the more dimorphic *Pongo* and *Gorilla*. The size distance between KNM-ER 1470 and OH 24 is 5.51. A distance of this magnitude is matched or exceeded by only 2 out of 3655 pairwise size distances in the modern human sample, and 41 of the 2415 pairwise distances in the chimpanzee sample ($p = 0.0008$ for modern *Homo* and 0.0174 for *Pan*). In the more dimorphic species a much larger proportion of the pairwise size distances exceed the distance between KNM-ER 1470 and OH 24. In *Pongo* 485 out of 2016 pairwise size D^2s are equal to or greater than the distance between the fossils ($p = 0.2411$), and in the *Gorilla* sample 751 of the 3486 possible distances exceed or match the distance between KNM-ER 1470 and OH 24 ($p = 0.2157$).

The results in Table 39 suggest that if KNM-ER 1470 and OH 24 are conspecifc the size difference between them may be due in large part to sexual dimorphism. In the chimpanzee sample 51% (21 out of 41) of the size distances between individuals that equal or exceed the distance between KNM-ER 1470 and OH 24 are between males and females, but in the other three reference samples a much larger proportion of these distances are between individuals of the opposite sex. For the modern humans both of the size distances that exceed the observed distance between the fossils are between males and females. In the

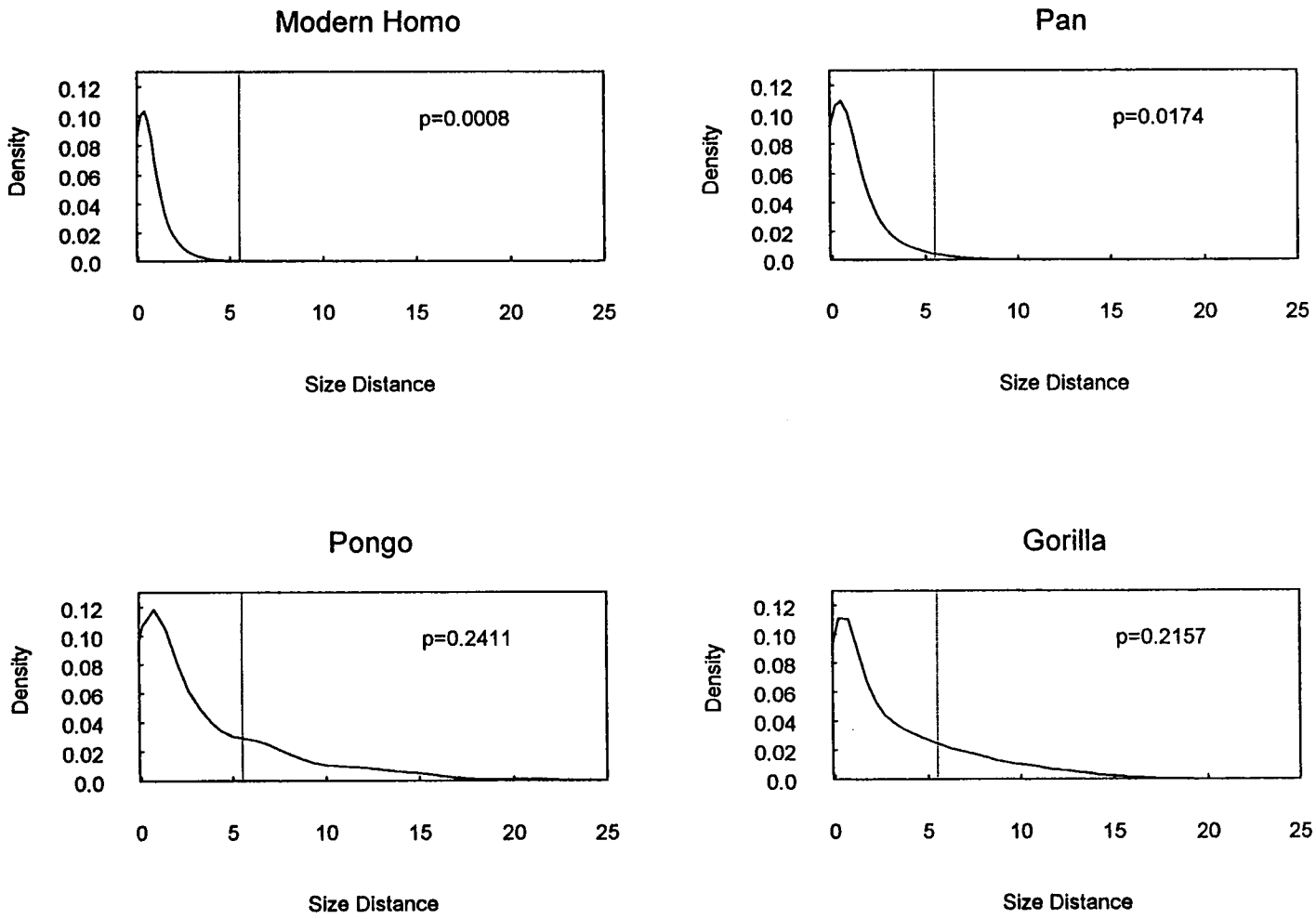


Figure 20. The smoothed distributions of all possible size distances between individuals in the reference samples plotted against the size distance between KNM-ER 1470 and OH 24 for the face. The vertical line shows the position of the distance between the fossils. ***p*** is the probability of finding a distance greater than the distance between the fossils in the reference distribution.

orangutan sample 88% (427 out of 485) and in the gorilla sample 99% (744 out of 751) of the distances that are equal to or larger than the distance between the KNM-ER 1470 and OH 24 are between males and females.

Comparisons with Plio-Pleistocene hominids

For the face the comparisons of the differences between KNM-ER 1470 and OH 24 with the differences between other Plio-Pleistocene hominids are based on the same measurements (FMB, EKB, OBB, OBH, IOB,NLB, NLH, NPH, MMH, MAB and PLB) and the same fossil hominids used in the comparisons of KNM-ER 1470 and 1813. In the fossil comparative group there are two pairs of fossils that are most likely conspecific: KNM-ER 406 and OH 5 which are most likely both male *A. boisei*, and Sts 5 and 71, which represent *A. africanus*.

In Table 25 (p. 199) the matrix of Mahalanobis distances between the Plio-Pleistocene hominids is shown and the descriptive statistics for the distributions of all possible pairwise distances in the modern hominoids are given Table 26. For KNM-ER 1470 and OH 24 the Mahalanobis D^2 is 40.45. This is larger than the all of the median distances for the modern reference groups, and for the modern humans it is larger than the upper 99th percentile and nearly equal to the maximum distance. For all three of the pongid samples however, the distance between KNM-ER 1470 and OH 24 is below the upper 95th percentile. When compared to the distances between other Plio-Pleistocene hominids the distance between KNM-ER 1470 and OH 24 does not appear to be unusually large. It is considerably larger than the distance of 26.61 between the two *A. africanus* crania, Sts 5 and Sts 71, but only slightly larger than the distance between OH 5 and KNM-ER 406 (38.98). It also falls within the range of distances between fossils that do not belong to the same species. It is larger than the distances between Sts 5 and KNM-ER 406 or OH 5 (35.78 and 32.72, respectively), but it is only slightly smaller than the distance between KNM-ER 406 and 3733 (42.78)

and it is much smaller than the distance between Sts 71 and KNM-ER 3733 (110.90) or between OH 5 and KNM-ER 3733 (67.77)

For the comparisons of the shape distances between Plio-Pleistocene hominids the results are very similar to those for the Mahalanobis distances. In Table 27 (p. 201) the matrix of shape distances between Plio-Pleistocene hominids is shown, and Table 26 gives the descriptive statistics for the distributions of pairwise shape distances within the modern reference groups. The shape D^2 between KNM-ER 1470 and OH 24 is 35.23. This distance exceeds the upper 99th percentile of the modern human sample, but it is below the upper 95th percentiles of the pongid distributions. The distance between KNM-ER 1470 and OH 24 also does not appear to be unduly large when compared to the shape distances between Plio-Pleistocene hominids. It is greater than the distance between Sts 71 and Sts 5 (26.54) but smaller than the distance between KNM-ER 406 and OH 5 (37.97). The distance between OH 24 and KNM-ER 1470 also falls within the range of distances for hominids that are not conspecific. Thus, it exceeds the shape distances between Sts 5 and KNM-ER 406 (29.75) or OH 5 (20.76) and is close to the distance between OH 5 and Sts 71, but it is smaller than the distances between the *A. africanus* or *A. boisei* faces and KNM-ER 3733.

In Table 29 (p. 202) the matrix of size distances between Plio-Pleistocene hominids is shown, and the descriptive statistics for the modern reference groups are presented in Table 30. When the size distance between KNM-ER 1470 and OH 24 of 5.21 is compared with the results in Table 30 it is apparent that the disparity in size between KNM-ER 1470 and OH 24 is large relative to the less dimorphic species, *Pan* and modern *Homo*, but not particularly large relative to *Pongo* or *Gorilla*. A size D^2 of 5.21 falls above the upper 99th percentile of the modern human sample and between the upper 95th and 99th percentiles of the chimpanzee sample but it is much smaller than the upper 95th percentiles for *Pongo* and *Gorilla*. When compared to the size distances between Plio-Pleistocene hominids the size distance between KNM-ER 1470 and OH 24 does appear to be very large. The size distance

of 5.21 is much larger than that between Sts 5 and Sts 71 (0.07) or between KNM-ER 406 and OH 5 (1.00). It is also larger than many of the distances between fossils that represent different species. For example, it is larger than the distances between KNM-ER 3733 and Sts 5 (3.78) or Sts 71 (2.83) and larger than the distances between KNM-ER 406 and Sts 71 (10.21) or KNM-ER 3733 (0.26) but it is not as large as the size distances between OH 5 and the gracile australopithecines, Sts 5 and Sts 71(11.96 and 10.21, respectively).

In Figure 10 (p. 204) the matrix of size distances between the fossils has been reduced to a single axis of variation. Here it is easier to see how the size difference between KNM-ER 1470 and OH 24 compare with size differences between other hominids. On this single size dimension the distance between KNM-ER 1470 and OH 24 is comparable to the distance between KNM-ER 406 and OH 5, and much larger than the distance between Sts 5 and Sts 71. It is also larger than the distance between KNM-ER 3733 and 406, or the distance between Sts 71 and KNM-ER 3733.

CHAPTER 9

MULTIVARIATE RESULTS: THE PHENETIC AFFINITIES OF KNM-ER 1470, KNM-ER 1805, KNM-ER 1813 AND OH 24.

As discussed in Chapter 3, if the hominids that have been attributed to *Homo habilis* actually represent more than one species their taxonomic affinities are very unclear. It is not even certain that they all belong in the genus *Homo*. The primary purpose of this dissertation is not to attempt a classification of the individual specimens. However, the results presented in Chapter 8 strongly suggest that there was more than one species of gracile hominid in East Africa during the Plio-Pleistocene and the possible affinities of these taxa and the individual specimens is an intriguing problem.

The multivariate distances between the Plio-Pleistocene hominids, which are used in Chapter 8 to compare the differences between the early *Homo* crania with the differences between other Plio-Pleistocene hominids, can also provide some insights on the phenetic and possibly the taxonomic affinities of the more complete early *Homo* specimens. The distances themselves can be used for this purpose, but a clearer picture of the phenetic affinities of the early *Homo* crania is gained by using principal coordinates analysis to reduce the distance matrices to a smaller number of dimensions and plotting the positions of the fossils in this reduced dimensional space. This is done for the matrices of Mahalanobis and shape distances given in Tables 18, 20, 25, 27, 32 and 34. For these matrices the first three principal axes account for approximately 99% of the variance in the original distance matrices and the positions of the fossils are therefore plotted in the derived three-dimensional space.

The phenetic affinities of the early *Homo* calvaria

The Mahalanobis distances between Plio-Pleistocene hominids shown in Table 18 (p. 185), which are based on measurements of the vault, suggest that the strongest affinities of the three early *Homo* specimens in the sample, KNM-ER 1470, 1813 and OH 24, are not

with one another, but rather with other taxa. The largest individual, KNM-ER 1470 is closest to the two *Homo erectus* specimens, KNM-ER 3733 and 3883. The Mahalanobis distance between KNM-ER 1470 and 1813 is 29.29, this is much larger than the distances between the former and KNM-ER 3733 (16.67) or 3883 (15.80). The smaller early *Homo* vaults however, are closer to the australopithecines. The shortest distances for KNM-ER 1813 and OH 24 are not to one another. For KNM-ER 1813 the shortest distance (25.88) is the distance to the gracile australopithecine, Sts 5, whereas OH 24 is closest to the female *A. boisei*, KNM-ER 407 ($D^2 = 9.11$), although it is also close to Sts 5 ($D^2 = 11.72$). The distance between KNM-ER 1813 and OH 24 is 28.99.

Comparisons of the shape distances (Table 20, p. 187) yield somewhat different results. With respect to shape KNM-ER 1813 is closest to KNM-ER 1470 ($D^2 = 16.39$) and OH 24 is closest to KNM-ER 407 ($D^2 = 8.83$) and Sts 5 ($D^2 = 11.30$). In terms of shape KNM-ER 1470 is closest to OH 24 (14.53) but this distance is only slightly smaller than the distance between KNM-ER 1470 and 3883 (15.26) or 1813 (16.39) or 3733 (16.65).

The phenetic affinities of these fossils are shown more clearly in Figures 21 and 22, which show the results of the principal coordinates analyses for the distance matrices in Table 18 and Table 20. The affinities of the fossils are summarized by fitting a minimum spanning tree (MST) to the points following Prim's (1957) algorithm. For all of the three dimensional plots showing the results of the principal coordinates analyses the first principal axis, which is the axis that accounts for the largest proportion of the variation in the original matrix, is the vertical axis, the second principal axis is the left to right horizontal axis and the third axis is the horizontal axis that extends from 'front to back'. It should be noted that for these figures the first three axes are all of the same relative length, even though they actually account for different amounts of the total variance in the distance matrices. That is, the length of an axis is not proportional to the amount of variance it accounts for.

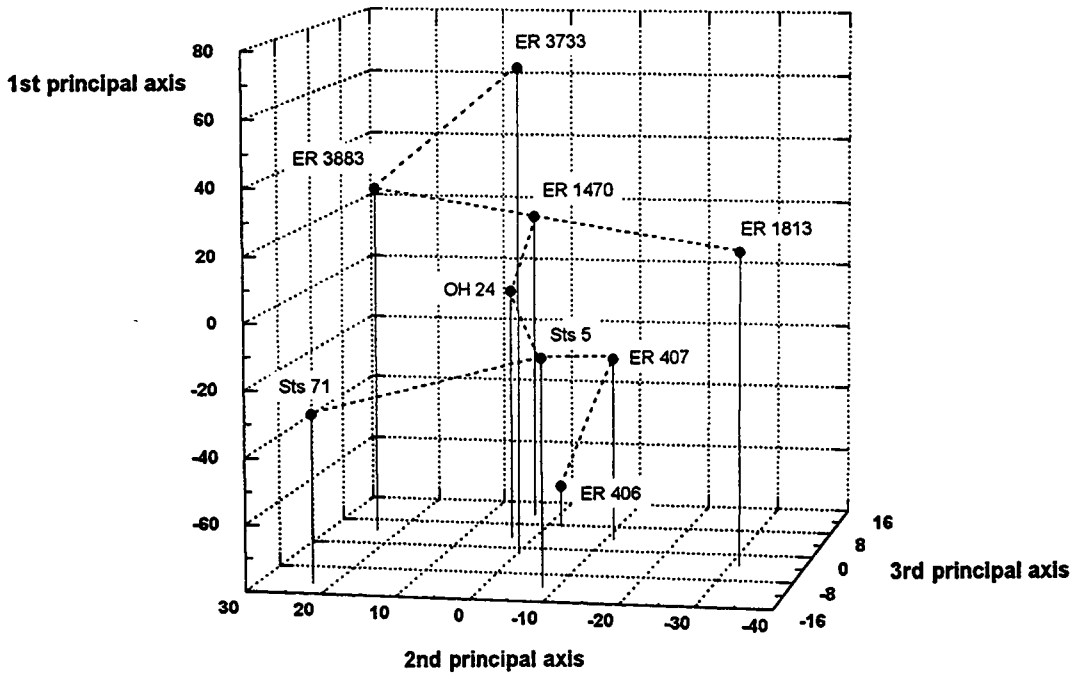


Figure 21. Minimum spanning tree and principal coordinates analysis of the Mahalanobis distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on calvarial measurements.

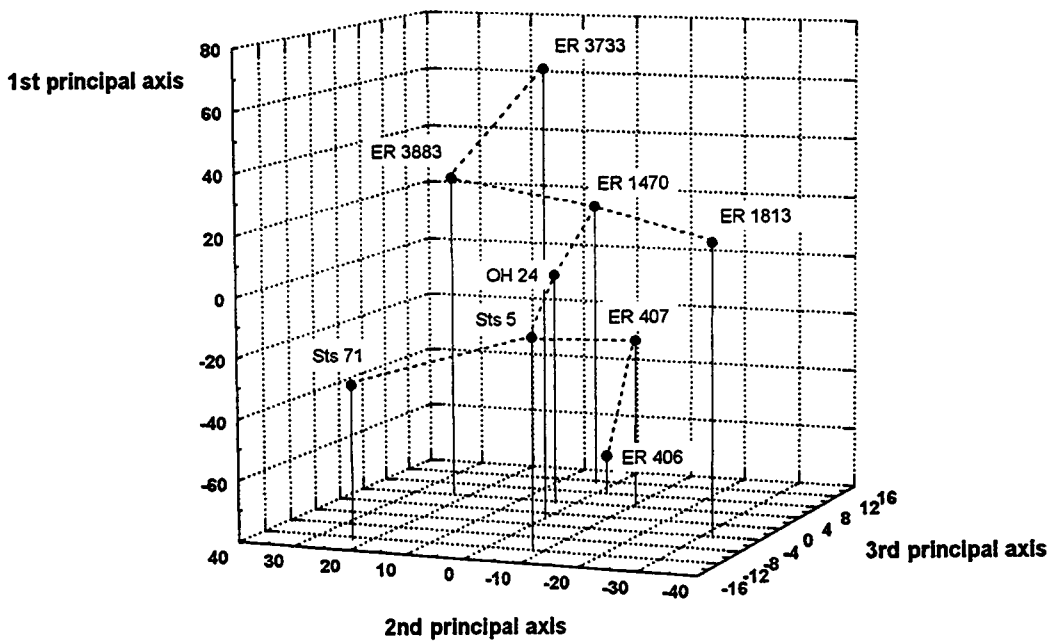


Figure 22. Minimum spanning tree and principal coordinates analysis of the shape distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on calvarial measurements.

It should also be noted that to show the positions of the fossils in three-dimensional space as clearly as possible the degree of vertical and horizontal rotation varies somewhat for each plot.

Because the results based on the Mahalanobis distances are very similar to those for the shape distances the two are discussed together. In both figures there is a clear separation between the *Homo erectus* vaults, KNM-ER 3733 and 3883, and the australopithecines on the first principal axis. KNM-ER 1470, 1813 and OH 24 occupy an intermediate position between these two groups. KNM-ER 1470 is located between the *Homo erectus* and the smaller early *Homo* vaults. In the MST it occupies a central position; it is linked with KNM-ER 3883, 1813 and OH 24. The latter is located between KNM-ER 1470 and the australopithecines and the MST connects it to both KNM-ER 1470 and to the gracile australopithecine, Sts 5. OH 24 is much closer to Sts 5 than it is to KNM-ER 1813. The latter is not particularly close to any hominid. Although the MST links it with KNM-ER 1470 it occupies an isolated position at the extreme lower end of the second principal axis.

When the multivariate distances are based on a different subset of measurements to allow for the inclusion of KNM-ER 1805 in the fossil sample the phenetic relationships of KNM-ER 1813 are altered. In the matrix of Mahalanobis distances in Table 32 (p. 212) KNM-ER 1813 is closest to KNM-ER 407 ($D^2 = 26.98$) and it is also closer to Sts 5 ($D^2 = 35.60$) than it is to KNM-ER 1470 ($D^2 = 44.74$). For the latter the closest affinities are with the *Homo erectus* vaults, KNM-ER 3733 ($D^2 = 22.89$) and KNM-ER 3883 ($D^2 = 20.52$) rather than with the two smaller early *Homo* crania. KNM-ER 1805 and 1813 are not close to one another ($D^2 = 61.50$). The former is closer to KNM-ER 1470 ($D^2 = 44.74$) than it is to KNM-ER 1813, but it is not particularly close to any hominid.

In the matrix of shape distances (Table 34, p. 214) the same basic pattern of relationships is evident. In terms of shape KNM-ER 1470 is much closer to KNM-ER 3733 or 3883 ($D^2 = 22.88$ and 20.24, respectively) than it is to KNM-ER 1813 or 1805 ($D^2 = 33.20$ and

34.21). For KNM-ER 1813 the closest affinities remain with the australopithecines and it is closer to KNM-ER 407 ($D^2 = 26.34$) than it is to the two other early *Homo* vaults. KNM-ER 1805 and 1813 are not close to one another ($D^2 = 61.41$) and for the latter the strongest affinities are with KNM-ER 1470.

The phenetic affinities of the early *Homo* vaults are seen more clearly in Figures 23 and 24. As in the previous analyses there is a clear separation of the *Homo erectus* and australopithecine vaults along the first axis. KNM-ER 1470 and 1805 occupy an intermediate position between the two groups, but KNM-ER 1813 is located with the australopithecines at the lower extreme of the first principal axis. In the MST KNM-ER 1470 again occupies an intermediate position, it is linked with KNM-ER 3733, 1805 and Sts 5, but KNM-ER 1813 is not directly linked with either of the other two early *Homo* specimens. Rather, it is located between the gracile australopithecine, Sts 5, and the female *A. boisei*, KNM-ER 407. Thus, for this set of measurements, which differs from the measurements used in previous analysis in excluding the measurements of frontal length (GBA and GBC) and including three additional dimensions of the parietals (XPB, SPC and LAC) KNM-ER 1813 shows the strongest phenetic affinities with the australopithecines. KNM-ER 1805 occupies an isolated position. It is linked with KNM-ER 1470 but it is not particularly close to any hominid.

The phenetic affinities of the early *Homo* faces

The matrix of Mahalanobis distances between Plio-Pleistocene hominids shown in Table 25 (p. 199) indicate that for the face the closest phenetic affinities of the larger and the smaller forms of early *Homo* specimens are not with one another. For the face the closest phenetic affinities of KNM-ER 1470 are with the robust australopithecines rather than with KNM-ER 3733. KNM-ER 1470 is closest to KNM-ER 406 ($D^2 = 22.44$) but this distance is nearly as large as the distance between KNM-ER 1470 and OH 5 ($D^2 = 24.18$) or KNM-ER

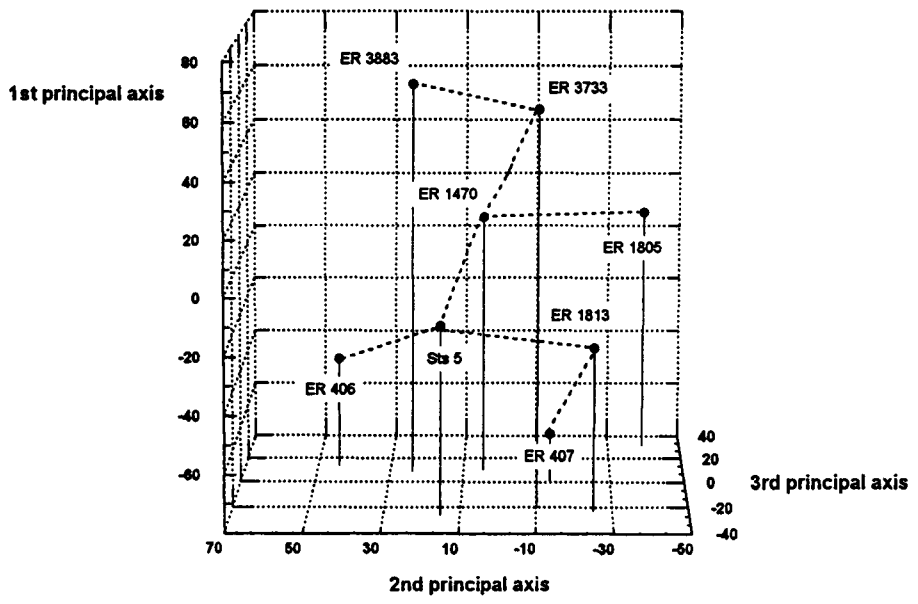


Figure 23. Minimum spanning tree and principal coordinates analysis of the Mahalanobis distances among KNM-ER 1470, KNM-ER 1813, KNM-ER 1805 and other Plio-Pleistocene hominids based on calvarial measurements.

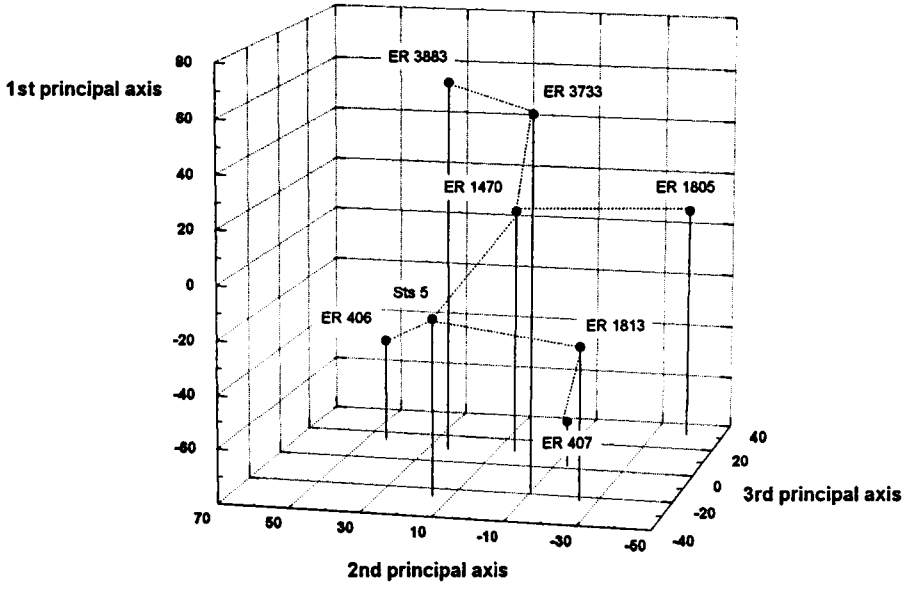


Figure 24. Minimum spanning tree and principal coordinates analysis of the shape distances among KNM-ER 1470, KNM-ER 1813, KNM-ER 1805 and other Plio-Pleistocene hominids based on calvarial measurements.

1470 and 1813 ($D^2 = 24.36$). The two smaller early *Homo* specimens are closer to one another than either is to any other hominid ($D^2 = 14.01$) and both are closer to Sts 5 than either is to KNM-ER 1470. The D^2 between KNM-ER 1813 and Sts 5 is 22.67, and for Sts 5 and OH 24 the D^2 is 37.43. These distances suggest that in terms of size and shape the closest phenetic affinities of KNM-ER 1470 are with the robust australopithecines, whereas for the smaller individuals the closest phenetic affinities are with gracile australopithecines.

A different pattern of relationships is seen in the shape distances between the fossils (Table 27, p. 201). KNM-ER 1813 and OH 24 are still closer to one another than either is to any other hominid ($D^2 = 13.79$), but the closest affinities of KNM-ER 1470 are now with KNM-ER 1813 rather than with the robust australopithecines. The shape distance between KNM-ER 1470 and 1813 is 16.81, whereas the distance between KNM-ER 1470 and KNM-ER 406 is 22.43, and the distance between the former and OH 5 is 23.43. The shape distances between KNM-ER 1470 and KNM-ER 406 or OH 5 are nearly equal to the Mahalanobis distances, whereas the Mahalanobis D^2 between KNM-ER 1470 and 1813 is much larger than the shape distance. This indicates that in terms of shape KNM-ER 1470 is more similar to KNM-ER 1813 than it is to robust australopithecines, and the overall resemblance of the KNM-ER 1470 face to KNM-ER 406 and OH 5 is due in large part to the fact that all of these specimens have large faces. For the shape distances KNM-ER 1813 and OH 24 are closer to KNM-ER 1470 than either is to Sts 5, although the distance between OH 24 and KNM-ER 1470 (35.23) is only slightly smaller than the distance between OH 24 and Sts 5 (37.36).

The phenetic affinities of the early *Homo* faces are represented more clearly in Figures 25 and 26. In both figures the pattern of relationships is nearly identical. The single *Homo erectus* specimen, KNM-ER 3733, occupies an isolated position; it is not close to any other specimen although the MST links it with KNM-ER 406. The three early *Homo* specimens are

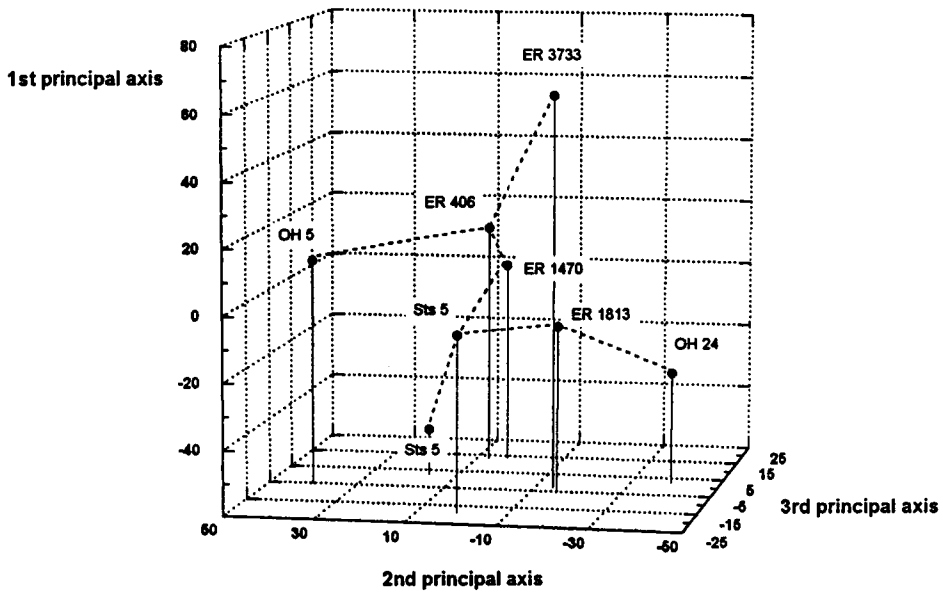


Figure 25. Minimum spanning tree and principal coordinates analysis of the Mahalanobis distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on facial measurements.

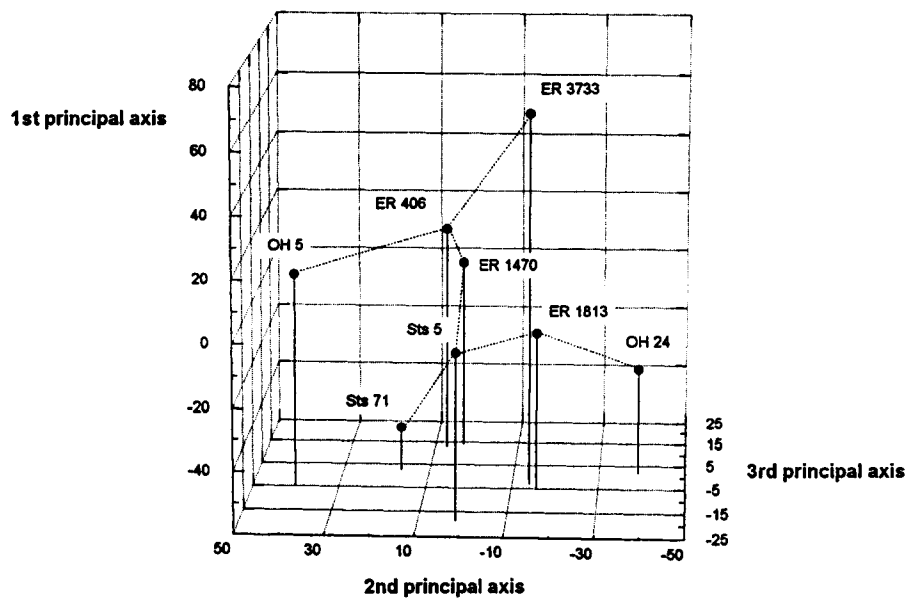


Figure 26. Minimum spanning tree and principal coordinates analysis of the shape distances among KNM-ER 1470, KNM-ER 1813, OH 24 and other Plio-Pleistocene hominids based on facial measurements.

all closer to the australopithecines than they are to KNM-ER 3733. KNM-ER 1470 is closestt o KNM-ER 406, and on the MST it is between this specimen and the gracile australopithecine, Sts 5. Neither KNM-ER 1813 nor OH 24 is directly linked with KNM-ER 1470. KNM-ER 1813 is located between Sts 5 and OH 24 and it connects the two. The latter specimen is isolated at one extreme along the second principal axis and its only direct connection is with KNM-ER 1813, which links it indirectly with Sts 5.

Thus, for the face the three early *Homo* specimens do not show the strongest phenetic similarities to one another; they do not appear to form a consistent, coherent cluster. The results of the principal coordinates analyses show that KNM-ER 1470 is most similar to the robust australopithecines whereas the smaller faces of KNM-ER 1813 and OH 24 are closest to Sts 5, a gracile australopithecine.

CHAPTER 10

DISCUSSION

Collectively, the results presented in the preceding three chapters strongly suggest that there is more than one species of early *Homo*. This conclusion is supported by the dental comparisons, the multivariate comparisons of KNM-ER 1470 with KNM-ER 1813, 1805 and OH 24, and the phenetic comparisons with the Plio-Pleistocene hominids that show that the larger and smaller forms of early *Homo* do not consistently cluster together, but rather show phenetic affinities to other hominids and different taxa. Each of these three lines of evidence is summarized and discussed in the following sections.

The magnitude and pattern of dental variation in early *Homo*

The results of the dental comparisons show that in the b-l diameters of the postcanine teeth there is a marked degree of variation in *Homo habilis*. This is evident in the CV profiles in Figures 1 and 2 (pp. 164 and 171) where it can be seen that the early *Homo* CVs are greater than all of the CVs for *A. robustus* and all but one of the CVs for *Pan* (the exception being P^3). In terms of magnitude the early *Homo* CVs are most similar to the *Gorilla* CVs, but even when compared to this sample several teeth seem to show an excessive degree of variation: for P_4, M^2 and M^3 the CVs for early *Homo* are even greater than those for *Gorilla*. However, the randomization test and the median log and median ratio tests demonstrate that most of the differences between early *Homo* and the reference groups in the degree of relative variation are not significant. The only consistently significant differences ($p<0.05$) are seen in P_4, where the degree of relative variation in early *Homo* is significantly greater than it is in any of the reference groups, and these differences are significant even when adjustments are made for multiple comparisons. For M^2 and M^3 the degree of relative variation in early *Homo* also appears to be significantly greater than it is in *Pan* and *A.*

robustus, but when a correction is made for multiple comparisons these differences are no longer significant, except for the difference between *Homo habilis* and *A. robustus* for M^3.

Overall the results of the dental comparisons do provide support for the multiple species argument. The degree of relative variation in the buccolingual diameter of P_4 for early *Homo* is significantly greater than it is in any of the reference groups, even the strongly dimorphic gorillas. This suggests that more than one species is represented in the collection of teeth that have been attributed to *Homo habilis*.

Groves (1989) and Wood (1991, 1993) have also found that for some dental measurements there appears to be an unusually large degree of variation in early *Homo*. Groves' (1989) assessment of dental variation in *Homo habilis* is difficult to evaluate or compare with this or other analyses because Groves does not identify the individual specimens included in his 'habiline' dental sample. The habilines are defined only as "Hominins with cranial capacities of more than about 530 but less than 800 cc, associated with large or medium-sized cheek teeth" (p. 192). In addition, Groves' (1989) analysis is limited to the mandibular teeth (C through M_2) and upper canines and he does not provide the CVs for individual measurements. According to Groves (1989) only the CVs for the upper canine of *Homo habilis* (14 and 16 for the m-d and b-l diameters, respectively) are 'suspiciously high'. These values fall within the range of CVs for apes, in which the upper canine shows marked sexual dimorphism, but according to Groves the habiline CVs are much larger than those of any of his other fossil hominid samples (*A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei* and *H. erectus*) and on the basis of this evidence he suggests that *Homo habilis* may represent more than one species. For the remaining dental measurements the habiline CVs fall within the range for living apes. The CVs are reported as 6-9 for P_3, and between 7-11 for P_4 - M_2. The CVs for the canines were not estimated here because of the small sample sizes, and the CVs obtained for P_3 and P_4 b-l (12.7 and 13.0) are larger than any of the CVs

reported by Groves (1989) for these teeth. These differences undoubtedly reflect differences in sample composition.

Wood (1991, 1993) also found that in *Homo habilis* there is a great deal of variation for some dental measurements. Unlike Groves, Wood (1993, Table 1, p. 486) identifies the specimens included in his *Homo habilis* sample, which consists of the same fossils used here, and also provides the measurements for them (Wood, 1991). Wood looked at variation in 52 measurements for both the maxillary and mandibular teeth: the m-d and b-l diameters for I1 through M3; crown areas of the canines, premolars and molars; length of the premolar tooth row; length of the molar tooth row; the combined areas of the premolars and the combined areas of the molars. Using the median log and median ratio tests for relative variation Wood identified two dental variables, the crown area of M_3 and m-d diameter of the lower canine, for which the degree of relative variation in the combined *Homo habilis* sample is significantly greater than the variation in at least one of his comparative samples (*Gorilla*, *A. boisei* and *Homo erectus*).

The results obtained here suggest that there is more variation in the early *Homo* dental sample than indicated by Wood's results. In particular, when compared to all three reference groups the degree of relative variation in the buccolingual diameter of P_4 is significantly greater in early *Homo*, and when compared to *Pan* and *A. robustus* the degree of relative variation in M^2 and M^3 b-l is also significantly greater in early *Homo*. Wood's results in contrast, do not suggest that the degree of variation is unusually large for any of these variables. These discrepancies may be due in part to the fact that Wood's dental sample and the dental sample used here are not equivalent, even though they include the same individuals. Wood's samples include both the left and right teeth for the same individual when both are present, whereas the sample used here includes only teeth from the left when both sides are represented. Thus, for this study the sample sizes are smaller. For P_3, for example, ***n*** is 13 in Wood's combined *Homo habilis* sample but it is only 9 in the sample

used here. Consequently, the CVs and other measures of variation are not equal for the two samples. For most variables the differences in the CVs are not large, but there are a few significant discrepancies, most notably for P_3 (Wood's CV is 14.0, the CV obtained here is 12.7), P_4 (Wood's CV = 11.7, the CV obtained here is 13.0) and P^4 (Wood's CV = 7.9, the CV obtained here is 6.3). In addition, with the exception of *Gorilla*, the two studies use different reference groups.

One of the characteristics cited by Leakey et al. (1964) as diagnostic of *Homo habilis* is buccolingual narrowing of the cheek-teeth which is most pronounced in the lower premolars and molars. According to Wood (1991,1993) however, this narrowing of the posterior teeth is found only in the smaller species of early *Homo*, which he identifies as *Homo habilis*. This species is represented by the fossils from Olduvai and the smaller individuals from Koobi Fora and Omo. In the larger species of early *Homo* (*H. rudolfensis*), which is not represented in the collection of fossils from Olduvai, the postcanine tooth crowns remain broad, as in *Australopithecus* (Wood, 1993, Table 16, p. 515). For Wood's combined *Homo habilis* sample the degree of variation in the postcanine b-l diameters is not unusually large, and the CVs for his Koobi Fora/Omo *Homo habilis* sample are also not particularly large. The results presented here however, indicate that for the width of some of the postcanine teeth the degree of relative variation in early *Homo* is very large for a single hominoid species, and this strongly suggests that multiple species are represented. Thus, these results support Wood's claim that there are two species of early *Homo* that can be distinguished on the basis of postcanine tooth breadth.

In addition there is another line of evidence which suggests that there might be more than one species of early *Homo*. The pattern of variation in the early *Homo* mandibular tooth sample appears to be distinctly different from the patterns of variation seen in the reference groups. This can be seen most clearly in Figure 1 where the CV profiles for the lower postcanine teeth of the early *Homo* and reference samples are depicted. The two

modern hominoids, *Pan* and *Gorilla* have CV profiles which are very similar in shape. For these two species the CV for P_3 is much higher than the CVs for P_4 - M_3 and there is a sharp drop in the CV profiles between P_3 and P_4. In both species the CVs for P_4 - M_3 fall within a relatively narrow range so for these teeth there are no sharp changes in the CV profiles. The CV profile for the single hominid reference species, *A. robustus*, follows a different pattern; all of the posterior teeth show approximately the same degree of relative variation, and thus the profile is relatively flat. In *A. boisei* and *Pongo* the CVs for P_3 and P_4 are also relatively small and nearly equal (Cole and Smith, 1987; Wood, 1993), and thus these species follow the pattern seen in *A. robustus*. In the early *Homo* sample however, the CVs for both P_3 and P_4 are large and nearly equal (12.7 and 13.0) and the CVs for the molars are much smaller (7.3 - 8.2). Thus, there is a sharp drop in the CV profile between P_4 and M_1. This is distinctly different from the pattern shared by *Pan* and *Gorilla* and it is also unlike the pattern seen in *A. robus*tus. These differences in the shape of the early *Homo* CV profile suggest that the early *Homo* dental sample either represents multiple species or a single species with a unique pattern of dental variation.

Size and shape variation in the face and vault of early *Homo*

The results of the multivariate comparisons with the modern hominoids provide the strongest evidence for multiple species of early *Homo*. These comparisons demonstrate that in both the vault and face the size differences, and in some cases the shape differences, between the largest early *Homo* specimen, KNM-ER 1470, and the smaller individuals, KNM-ER 1805, 1813 and OH 24, are large when compared to the differences in size and shape seen in the extant hominoids and it is unlikely that KNM-ER 1470 and the smaller specimens could all represent the same species unless that species were more sexually dimorphic than *Gorilla*. Even if *Homo habilis* were as dimorphic as gorillas the probability of finding size differences as large as those seen between KNM-ER 1470 and the smaller specimens is quite small.

Furthermore, the size differences between KNM-ER 1470 and the smaller crania are also quite large when compared to the size differences between fossil hominids that are generally regarded as conspecific, and they are often large when compared to the size differences between fossil hominids that undoubtedly represent different species. Collectively, the comparisons with the modern hominoids and the fossil hominids provide strong evidence that there is more than one species of early *Homo*.

Comparisons of the differences between KNM-ER 1470 and 1813 with the differences between individuals in the modern reference samples demonstrate that it is unlikely that these two fossils could represent the same hominoid species. The most marked differences between them are in the vault where the comparisons with the modern hominoids, using the Mahalanobis D^2 as the measure of distance, show that the probability that these two fossils could be derived from a single species is small. Even in the gorilla sample the probability of randomly sampling two individuals separated by a D^2 equal to or greater than the distance between KNM-ER 1470 and 1813 is only 0.11 (Table 17, p. 176). The differences between KNM-ER 1813 and 1470 in the face however, are not nearly as large as the differences in the vault. For the face the multivariate distance between the fossils is large only when compared to the distances between modern humans. In each of the pongid samples a large proportion (40 - 60%) of the pairwise D^2s between individuals are equal to or greater than the D^2 between KNM-ER 1470 and 1813 (Table 24, p. 192).

When the multivariate distances between the fossils are partitioned into their size and shape components, comparisons with the modern reference groups show that the size disparity between KNM-ER 1470 and 1813 is exceptionally large for two individuals who belong to the same hominoid species. With respect to shape the differences between KNM-ER 1470 and 1813 in the vault are large but they are not as pronounced as the size differences, whereas the shape differences in the face are not particularly large at all.

The size differences in the vault are so great that it is seems unlikely that KNM-ER 1470 and 1813 could be derived from the same species, unless that species were as dimorphic as modern gorillas, a species in which males weigh more than twice as much as females (Fleagle, 1989; Leutenegger and Cheverud, 1982, 1985). However, even if *Homo habilis* were as dimorphic as gorillas the probability of randomly sampling two individuals as disparate in size as KNM-ER 1470 and 1813 is less than 0.10. The comparisons with other Plio-Pleistocene hominids also demonstrate that the size differences between KNM-ER 1470 and 1813 are large relative to the size differences found between fossils that are conspecific and they are also large when compared to the size distances between fossils that represent different species. For the vault the size distance between KNM-ER 1470 and 1813 is much larger than any of the distances between fossils that are conspecific, exceeding the size distances between KNM-ER 406 and 407, between Sts 5 and Sts 71, and between KNM-ER 3733 and 3883. The distance between KNM-ER 1470 and 1813 is also larger than many of the distances between fossils that represent different species, e.g. it is larger than the distances between the *A. boisei* and *Homo erectus* vaults, larger than the distances between the *A. boisei* and *A. africanus* vaults and larger than the distances between Sts 5 and the two *Homo erectus* vaults. Only the size distances between Sts 71 and KNM-ER 3733 and 3883 are as large as, or larger than, the size distance between KNM-ER 1470 and 1813. For the face the size distance between KNM-ER 1470 and 1813 is also large when compared to the size differences seen in the modern reference samples and when compared to the size distances between conspecific fossil hominids, (i.e. KNM-ER 406 and OH 5; Sts 5 and 71). This distance is also larger than most of the size distances between fossils that are not conspecific. Only the size distances between OH 5, which has a very large face, and the two gracile australopithecines, Sts 71 and Sts 5, which have small faces, are larger than the distance between KNM-ER 1470 and 1813.

The comparisons of KNM-ER 1470 and 1805 with the modern hominoids yield results very similar to those for KNM-ER 1470 and 1813. The Mahalanobis distance between the fossils is very large and not likely to be found between individuals that are conspecific, even in a species as sexually dimorphic as gorilla (p = 0.09). The probability of finding a pairwise distance as large or larger than the Mahalanobis D^2 between KNM-ER 1470 and 1805 in the less dimorphic orangutans and chimpanzees is even smaller and it is very small for modern *Homo*. When the multivariate distance between KNM-ER 1470 and 1805 is partitioned into its size and shape components the comparisons with the modern hominoids show that the shape difference between the fossils is large relative to the modern reference groups, and the probability of finding a shape distance of that magnitude in a species as dimorphic as *Homo* or *Pan* is small, and even in the more sexually dimorphic orangutans and gorillas the chances of seeing a larger shape distance are still relatively small (p=0.09 for *Pongo* and 0.12 for *Gorilla*). The size differences between KNM-ER 1470 and 1805 are even more pronounced than the shape differences. The probability of seeing a size difference as large as the difference between KNM-ER 1470 and 1805 is very small for a species as dimorphic as *Homo*, *Pan* or *Pongo*, and even in the *Gorilla* sample the probability of seeing a size distance of that magnitude or greater is less than 0.10. Comparisons with other fossil hominids show that the size distance between KNM-ER 1470 and 1805 is much larger than the size distances between conspecific hominids such as KNM-ER 406 and 407, or KNM-ER 3733 and 3883. The size distance between KNM-ER 1470 and 1805 is also as large as, or larger than, all but one of the size distances between fossils that belong to different species. Only the size distance between the gracile australopithecine Sts 5 and the KNM-ER 3733 *Homo erectus* cranium is appreciably larger than the size distance between KNM-ER 1470 and 1805. Overall, the comparisons with the modern hominoids and the fossil hominids demonstrate that it is unlikely that two individuals as disparate in size and shape as KNM-ER 1470 and 1805 could be derived from the same hominoid species.

If the two fossils do represent the same species however, the size differences between them are almost certainly due to sexual dimorphism; the larger KNM-ER 1470 would be a male and the smaller KNM-ER 1805 a female. This however, is difficult to reconcile with the morphology of the latter. Although the vault of KNM-ER 1805 is small when compared to KNM-ER 1470 the parasagittal crests, well-developed compound temporonuchal crests and extensive pneumatization of the cranial base are all features which indicate that this individual was quite robust, and in modern pongids these features are much more likely to be seen in males than in females.

Multivariate comparisons with the modern reference samples show that the size differences between OH 24 and KNM-ER 1470 in the vault and face are large when compared to the two least dimorphic species, modern *Homo* and *Pan*. However, they are not as extreme as the size differences between KNM-ER 1470 and 1813, or between KNM-ER 1470 and 1805. Furthermore, the differences in the shape of the face are large when compared to the shape differences seen in the reference groups. In the discussion that follows it is important to bear in mind the fact that the vault of OH 24 is somewhat distorted, and the results of the comparisons of the vault should be interpreted with caution.

For the vault the Mahalanobis distance between the fossils is large when compared to modern *Homo*, but in the orangutan or gorilla samples the distance between the fossils is exceeded by a large proportion of the distances between individuals. The differences in the face are more salient than those in the vault. For the face the Mahalanobis distance between KNM-ER 1470 and OH 24 is very large compared to modern *Homo* ($p < 0.01$) and although it is not as extreme relative to the distances within the pongids, even in the strongly dimorphic gorillas the probability of seeing a Mahalanobis distance of that magnitude or greater is only ~0.11.

When the multivariate distances between KNM-ER 1470 and OH 24 are partitioned into their size and shape components comparisons with the modern hominoids show that the

shape differences in the vault are large relative to the shape differences seen in modern *Homo*, but not especially so when compared with *Pan*, *Pongo* or *Gorilla*. The size distance between KNM-ER 1470 and OH 24 for the vault is also large only when compared to modern *Homo*, and perhaps *Pan*; in the orangutan and gorilla samples a much larger proportion of the pairwise size distances between individuals equal or exceed the distance between the fossils. Thus, the size and shape differences in the vault indicate that KNM-ER 1470 and OH 24 could be conspecific if they represent a species as dimorphic as *Pongo* or *Gorilla* but they are less likely to be derived from a less dimorphic species such as *Pan* or modern *Homo*. The size and shape differences between KNM-ER 1470 and OH 24 in the face are more pronounced than the differences in the vault. For the face the probability of seeing a shape distance greater than the distance between KNM-ER 1470 and OH 24 is very small for a species as dimorphic as modern *Homo*, and although it is larger in the pongids, it is still relatively small. Even in a species as dimorphic as *Gorilla* the probability that a shape distance between two individuals would be as large as, or larger than, the shape distance between KNM-ER 1470 and OH 24 is only 0.12. When compared with the less dimorphic species, *Pan* and *Homo*, the size differences between KNM-ER 1470 and OH 24 are even more pronounced than the shape differences. However, for the more dimorphic *Pongo* and *Gorilla* the size difference between the fossils is not particularly large and the probability of finding two individuals as different in size as KNM-ER 1470 and OH 24 in a species as dimorphic as orangutans or gorillas is greater than 0.20.

Comparisons with other Plio-Pleistocene fossil hominids also show that the size differences between KNM-ER 1470 and OH 24 are quite large for individuals who are conspecific. For the face and vault the Mahalanobis and shape distances between KNM-ER 1470 and OH 24 are not as large as the equivalent distances between conspecific hominids, e.g. KNM-ER 406 and 407, KNM-ER 3733 and 3883, or Sts 5 and 71. However, the size distances for the face and vault are large when compared to the size distances between conspecific fossil

hominids. For both the vault and face the size distances between KNM-ER 1470 and OH 24 are larger than any of the size distances between conspecific hominids, and in many cases these distances are larger than the distances between fossils that are not conspecific. This is particularly true for the face where the distance between KNM-ER 1470 and OH 24 is exceeded only by the distances between OH 5 and the two gracile australopithecines.

The comparisons with the modern hominoids and the fossil hominids demonstrate that it is unlikely that KNM-ER 1470 and the smaller early *Homo* crania could all represent *Homo habilis*. The size differences between them in the face and vault are simply too great to allow for the comfortable attribution of all of these fossils to the same species. Even if *Homo habilis* were as sexually dimorphic as modern gorillas the size differences between KNM-ER 1470 and the smaller crania are so great that the probability of randomly sampling two individuals that are so different in terms of size from one species is quite low.

The results of the multivariate comparisons with the modern hominoids are in broad agreement with the results of previous studies by Lieberman et al. (1988), Wood (1991, 1993) and Kramer et al. (1995) that have taken a probabilistic approach, or used multivariate statistics, or both, to address the question of taxonomic heterogeneity in *Homo habilis*. Lieberman and his colleagues (1988) were the first to take a probabilistic approach in attempting to resolve the '*Homo habilis* problem'. Their study was limited to comparing the two most complete, and also the most disparate, *Homo habilis* crania, KNM-ER 1470 and 1813. Their analysis was also limited to univariate comparisons of individual measurements using the index of dimorphism (I_d) as the test statistic, and *Gorilla* was the only reference group with which the fossils were compared. Their rationale for using gorillas as the comparative group is that they are the most sexually dimorphic of hominoids and so are the most 'conservative' reference sample against which the differences between KNM-ER 1470 and 1813 can be compared. Lieberman et al. also assumed that KNM-ER 1470 and 1813 are male and female, respectively, and the differences between them are primarily due

to sexual dimorphism. For each of their 27 cranial measurements Lieberman et al. compared the I_d for KNM-ER 1470 and 1813 with the I_ds for 20 randomly chosen male-female pairs of gorillas. For 8 of the 27 variables the differences between KNM-ER 1470 and 1813 were not matched or exceeded by any of the twenty randomly chosen pairs of male-female gorillas. On the basis of these results the authors concluded that even if *Homo habilis* were as sexually dimorphic as modern gorillas it is unlikely that KNM-ER 1470 and 1813 could both represent that species. The size differences between them are simply too great.

Rather than assuming that KNM-ER 1470 must be male and KNM-ER 1813 (as well as KNM-ER 1805 and OH 24) must be female the multivariate comparisons between KNM-ER 1470 and the smaller crania are used here to test this assumption. This is a supposition that often serves as the foundation on which discussions of cranial variation in *Homo habilis* are based (e.g. Lieberman et al., 1988; Wood, 1985, 1991, 1993; Rightmire 1993). The multivariate comparisons with the modern hominoids show that, *if* they did all represent one very sexually dimorphic species, the differences between KNM-ER 1470 and KNM-ER 1805, 1813 and OH 24 would almost certainly have to be due to sexual dimorphism. The larger KNM-ER 1470 would be a male and the smaller KNM-ER 1813, 1805 and OH 24 would be females. It is highly unlikely that differences as large as those between the larger and smaller early *Homo* crania would be seen in individuals of the same sex in any hominoid species.

The results of the multivariate comparisons with the modern hominoids are generally consistent with the results obtained by Lieberman et al. (1988) and support their conclusions. However, the multivariate comparisons show that the size differences between KNM-ER 1470 and 1813 are not as extreme as their univariate comparisons would seem to suggest. Lieberman et al. interpreted their results as evidence that KNM-ER 1470 and 1813 are unlikely to belong to the same species because for some variables the size differences between them are so great that they are not matched or exceeded by the size differences

between any of the male-female gorilla pairs. The results presented here demonstrate that when a multivariate measure of size is used the differences between KNM-ER 1470 and 1813 can be matched or exceeded by a small proportion of the size differences between male and female gorillas and it is even exceeded by a very small proportion of the size distances between females and females and between males and males. The size disparity between KNM-ER 1470 and 1813 can be matched or exceeded in a hominoid as dimorphic as *Gorilla*, and thus it is within the realm of possibility that KNM-ER 1470 and 1813 could both belong to *Homo habilis* if *Homo habilis* were as dimorphic as gorillas. It is not impossible, but it is not probable.

Based on the pattern of the differences between KNM-ER 1470 and 1813 Lieberman et al. (1988) argued that there are important shape differences between the two which cannot be explained by sexual dimorphism and do not support their inclusion in the same species. This argument was first advanced by Wood (1985) and Rightmire (1993) has advanced a similar argument, claiming that the pattern of differences between the larger and smaller early *Homo* crania is more suggestive of taxonomic variation than sexual variation. Wood (1991, 1993) attempted to demonstrate this by using multivariate statistics to compare the differences between KNM-ER 1470 and 1813, and KNM-ER 1470 and OH 24, with the differences between males and females in modern hominoids. Using canonical variates analysis he compared the multivariate relationships between the fossil crania with those of separate sex samples of extant large-bodied hominoids. When KNM-ER 1470 and OH 24 are compared with one another in this manner (Wood, 1993, Fig. 4, p. 504) the slope of the line joining the fossils appears to be nearly orthogonal to the lines connecting the male and female centroids of *H. sapiens*, *Pan* and *Gorilla*, and it is oblique to the line connecting the male and female orangutans. A similar pattern of relationships appears when KNM-ER 1470 and KNM-ER 1813 are compared in the same way.

According to Wood these comparisons indicate that KNM-ER 1470 and the smaller crania are unlikely to be conspecific because the differences between them do not conform to the differences that distinguish males and females in modern hominoid species. Wood's interpretation can be questioned however, because as noted in Chapter 4, the differences between individuals are compared with the differences between the centroids for the modern hominoids. Comparisons of this sort are valid only if it is assumed that KNM-ER 1470 is a 'typical' male, and KNM-ER 1813 and OH 24 are 'typical' females of their species. The methods used here do not depend upon such assumptions, and by comparing the differences between pairs of fossils with the differences between pairs of individuals in modern hominoids the significance of the size and shape differences between the fossils are evaluated in terms of probabilities.

The results of this study do provide some support for Wood's conclusions concerning the pattern of differences between KNM-ER 1470 and KNM-ER 1813 and OH 24. The multivariate comparisons with the modern hominoids show that the shape differences between some of the early *Homo* specimens are large, particularly the shape differences between KNM-ER 1470 and 1805 and the differences between KNM-ER 1470 and OH 24 in the shape of the face, and the probability of matching or equalling these differences in the reference samples is low. However, for many of the comparisons the shape differences are not so large that we can completely exclude the possibility that the fossils could be conspecific. If these comparisons were made within a framework of hypothesis testing and a significance level of 0.05 were used as the criterion for accepting or rejecting the single species hypothesis, most of the shape differences between the fossils would be considered insignificant. There are two possible explanations for why the results obtained here provide only equivocal support for the argument that the shape differences between KNM-ER 1470 and the smaller crania reflect taxonomic variation rather than sexual dimorphism. It is likely that both are relevant.

The first possibility is that there is more variability, both within and between the sexes, in the traits that supposedly distinguish males from females than is commonly recognized and consequently comparing the differences between individual fossils with the differences between a hypothetical 'typical' male hominoid and a hypothetical 'typical' female is misleading. For example, while it may be true that in hominoids the average male exhibits more subnasal prognathism than the average female, there is no reason to believe, and no justification for assuming, that KNM-ER 1470 is an average male, or that KNM-ER 1813 is an average female. It may be that the probability of randomly sampling a male as orthognathic as KNM-ER 1470 and a female as prognathic as KNM-ER 1813 from a single hominoid species is very small, in which case there would be a justification for arguing that the two are probably not conspecific. On the other hand this probability may be relatively large, in which case we could not rule out the possibility that they are conspecific.

The second possibility is that the shape distances being compared here simply do not capture or adequately represent the shape differences that distinguish males and females in modern hominoids. Many of the features that supposedly distinguish males from females, such as the development and prominence of the supraorbital tori, the placement of the maxillary root of the zygomatic and the degree of subnasal prognathism, are not measured here. In addition, all but two of the variables used in the multivariate comparisons are cord distances between landmarks; subtenses and cord fractions, which would provide a better picture of cranial and facial shape, are not used.

The results obtained here are consistent in many respects with the results of the study by Kramer et al. (1995), the only previous analysis that has used both multivariate statistics and a probabilistic approach to attempt a resolution of the '*Homo habilis* problem'. This is hardly surprising since this dissertation is an extension and elaboration of our earlier work. In the interpretation of our results however, we reached different conclusions about the magnitude and pattern of cranial variation in early *Homo*.

We interpreted the results of our univariate and multivariate analyses as evidence that the magnitude of variation in *Homo habilis* is not excessive when compared to the variation seen in the more dimorphic great apes, *Pongo* and *Gorilla*. Therefore, we argued that the degree of craniometric variation in early *Homo*, that is the differences in size, are not large enough to justify rejecting the null hypothesis of a single species. However, on the basis of our comparisons of the CV profile for early *Homo* with the CV profiles of the reference species, we claimed that the pattern of variation (i.e. differences in shape) in early *Homo* is unlike the pattern of variation shared by all modern hominoids, and based on the apparent differences in shape we concluded that there is probably more than one species of early *Homo*.

In contrast the results obtained here suggest that it is the size differences between KNM-ER 1470 and the smaller crania that provide the strongest evidence of multiple species of early *Homo*. The results of the shape comparisons are more ambiguous. Some of the shape differences between KNM-ER 1470 and the smaller specimens are so large that it is unlikely that they would be seen in individuals that belong to the same species. For example, the shape differences between KNM-ER 1470 and 1805 in the vault, or between KNM-ER 1470 and OH 24 in the face are much larger than the shape differences between individuals in the modern reference groups. However, some of the shape differences between KNM-ER 1470 and the smaller specimens are not unusually large and could easily be found in two individuals that are conspecific.

The differences in interpretation are due in part to the fact that in our earlier paper we took a strict hypothesis testing approach to the problem and therefore we considered distances which are large relative to the distances seen in the reference samples but which had p-values larger than 0.05, to be nonsignificant. In contrast the approach taken here is one of simply estimating probabilities with little concern for strict hypothesis testing. Although the results obtained here are interpreted differently they do agree with the results

of the multivariate comparisons in our earlier study. In both cases the pooled within-groups variance-covariance matrix of the reference groups is used to find the multivariate distances between the fossils and between individuals in the reference samples. Therefore, it is not surprising that the results of our comparisons of the total multivariate distances between the fossils, estimated from summed weighted principal component scores, are similar to the results obtained here for the comparisons based on the Mahalanobis distances. In addition, our results for the distance comparisons between the fossils on the first principal components are similar to the results obtained here for the size distances. In the study by Kramer et al. the largest multivariate distances between KNM-ER 1470 and 1813 and between KNM-ER and OH 24 were on the first principal components, whereas in this study it is the size differences between the fossils that are most pronounced. Since Burnaby's method of size correction uses the first principal component of ***W*** as the size factor whose influence is removed from the Mahalanobis distance, this agreement in the results is not surprising. However, the results of this study show that the size differences between KNM-ER 1470 and the smaller crania are more extreme than our previous results suggest, although many of these size differences would be considered 'nonsignificant' in the context of strict hypothesis testing.

In our earlier paper we felt that the pattern of craniofacial variation in early *Homo* provided the strongest evidence of taxonomic heterogeneity. This claim was based on the results of our comparisons of the early Homo CV profile with the CV profiles of the modern reference groups. In contrast, the results of this study suggest that the size differences between KNM-ER 1470 and the smaller crania are the strongest evidence for multiple species. The method used here of extracting a shape distance from the Mahalanobis D^2 between two individuals is a more direct way of looking at shape variation. In our comparisons of the CV profiles we compared the CV profile for early *Homo* with the mean CV profiles, generated by randomization, of the reference species. We were, in effect, assuming

that the early *Homo* CV profile is an accurate representation of the pattern of variation in early *Homo*. Given the fact that the sample sizes were small for all of the craniometric variables (the largest ***n*** for any variable is 7 and the smallest ***n*** is 2) this is a questionable assumption. The results obtained here, using a more direct measure of shape variation and a more appropriate method of comparing shape differences, are more ambiguous, but they do provide some support for our previous claims about the pattern of craniometric variation in early *Homo*. The differences in the results may be due in part to the methods used but they may also be due to differences in sample composition. In this study the shape comparisons are between individual early *Homo* faces and calvaria, whereas in our earlier study we were looking at shape variation in all of the cranial specimens for which measurements are available. Another possible factor that may account for the differences in the results of the shape comparisons is the fact that the vault and face are treated separately in this study, but were combined in our earlier study. It may be the case that the unusual pattern of shape variation revealed by the comparisons of the CV profiles reflects unusual differences in the size of the vault relative to the size of the face in the early *Homo* sample. In modern hominoids there appears to be more variation in the face than in the vault. Thus, for example, if KNM-ER 1470 and 1813 both represent the same species, and if that species conforms to the pattern of variation seen in the modern large-bodied hominoids, the size differences in the face should be greater than the size differences in the vault. Instead, it appears to be the case that there are marked differences in the size of the face and in the size of the vault. This unusual pattern would be reflected in the CV profiles, where facial and calvarial measurements are combined, but not in the shape comparisons made in this study because the face and vault are treated separately.

In this dissertation and in the earlier study by Kramer et al. variation in the early *Homo* crania is compared with variation in all of the modern large-bodied hominoids except *Pan paniscus*. The rationale for using these reference samples is described in Chapter 5, but

within the four reference species, modern *Homo*, *Pan*, *Pongo* and *Gorilla*, there is a wide range of variation in the degree of sexual dimorphism in body size. Humans are the least dimorphic species, with males weighing ~20% more than females, and gorillas are the most dimorphic, with males weighing more than twice as much as females (Fleagle, 1988). Not surprisingly, in the multivariate comparisons with the modern hominoids the relative magnitude of the differences between the fossils depends on the modern reference group with which they are being compared. Multivariate differences that are very large relative to the differences seen in modern *Homo* or *Pan* are not nearly so large when compared to the differences seen in *Pongo* and *Gorilla*. Many of the differences between KNM-ER 1470 and the smaller crania are so great that it is very unlikely that they could all represent the same species if that species were as sexually dimorphic as modern *Homo* or *Pan*. But if *Homo habilis* were as dimorphic as *Pongo* or *Gorilla* it is more probable, although in some cases the probability is not especially large, that the fossils could be conspecific.

In the past ten years there has been a great deal of interest in estimating body sizes for early hominids (e.g. Aiello and Wood, 1994; Hartwig-Scherer, 1993; Jungers, 1988; McHenry, 1988, 1991, 1992, 1994). These estimates, based as they are on fragmentary and incomplete fossils, different measurements and different statistical methods, have produced widely divergent estimates of stature and body mass for early hominids. However, all of these studies do show that in early *Homo* there is a great deal of variation in body mass and stature, and if there was only one species of early *Homo*, it was probably more like *Pongo* and *Gorilla*, and less like *Pan* and modern *Homo*, in the degree of body size dimorphism. McHenry (1988, 1992), using the cross-sectional area of the femur as the predictor variable, obtained body size estimates that ranged from 33 to 57 kg (McHenry, 1988) and 39 to 52 kg (McHenry, 1992) for a sample of four early *Homo* femora. Hartwig-Scherer (1993), using a different set of predictor variables, obtained estimates that were between 22 or 28 and 49 kg for a sample of three early *Homo* femora. These estimates

demonstrate there is a considerable range of variation in body size in these very small samples. According to McHenry (1991) the 'large morph' of early *Homo* (which could represent either *Homo habilis* males or *Homo rudolfensis*) has an average estimated body mass of 52 kg ($n = 2$) whereas for the smaller morph (which could be *Homo habilis* females or *Homo habilis* as defined by Wood) the average estimated body mass is 32 kg ($n = 2$).

These averages undoubtedly have large standard errors, based as they are on small samples and imprecise estimates. Nevertheless, when they are compared with the averages for modern hominoids they suggest a gorilla or orangutan degree of sexual dimorphism. For example, the ratio of male to female mean body mass is 2.47 for gorillas, 1.9 for orangutans, ~1.25 for both *Pan troglodytes* and *P. paniscus*, and 1.05 for modern *Homo* (data from McHenry, 1988). For McHenry's estimated averages for the large and small forms of early *Homo* the ratio is 1.6. This is considerably larger than the ratios for modern *Homo* and *Pan*, but smaller than those for *Pongo* and *Gorilla*. The ratio for early *Homo* is estimated using estimates of body mass and this contributes an additional degree of uncertainty to the ratio for early *Homo*.

If the degree of imprecision is reduced by using the cross-sectional area of the femur as a surrogate for body size the differences between the large and small forms of early *Homo* become even more like those between males and females in *Gorilla* and *Pongo*. The ratio of the male to female means for the cross-sectional area of the femur is 1.5 for *Pongo* and *Gorilla*, 1.3 for modern *Homo*, and ~1.1 for *Pan* (McHenry, 1988). For early *Homo* there are three femora for the large morph (mean cross-sectional area = 678 mm^2) but only 1 for the small morph. This is OH 62, for which the estimated cross-sectional area of the femur is 441 mm^2 (McHenry, 1988). The ratio of the average area for the large morph with the area for OH 62 is 1.5, identical to the ratios for gorillas and orangutans. The ratio for early *Homo* should be regarded with caution because there is only one femur for the small morph, and it could be case that OH 62 is simply an unusually small female. Nevertheless, if the

large and small morphs represent males and females of *Homo habilis*, the large ratio does suggest a degree of sexual dimorphism comparable to that seen in gorillas and orangutans for *Homo habilis*.

Both Wolpoff (1996) and Miller (1994, 1995) have suggested that a gorilla- or orangutan-like degree of sexual dimorphism is not unreasonable for *Homo habilis*. However, Leutenegger and Cheverud (1982, 1985) have shown that body size has a major effect on body size dimorphism in primates. In fact, they found that "(v)ariation in body weight dimorphism can be almost entirely attributed to body weight (83% of variance R^2 of weight dimorphism" (Leutenegger and Cheverud, 1985, p. 48). Although the estimated body weights for early *Homo* are imprecise, the *largest* estimate is for KNM-ER 1472, with an estimated body weight of 49 kg according to Hartwig-Scherer (1993) and 52 or 53 kg according to McHenry (1988, 1992), and the average for early *Homo* was perhaps ~42 kg (McHenry, 1994). Both the mean and the maximum are far below the gorilla range of 75 to 180 kg, and they are at the lower end of the range for *Pongo* (Leutenegger, 1977). In terms of body size early *Homo* was much smaller than *Gorilla* and considerably smaller than *Pongo*. If body size is the primary determinant of sexual dimorphism in primates, as Leutenegger and Cheverud (1982, 1985) have demonstrated, it does not seem likely that a hominoid as small as early *Homo* would show as much sexual dimorphism as modern gorillas.

The phenetic affinities of the gracile East African hominids

In the phenetic comparisons of the early *Homo* crania with other Plio-Pleistocene hominids, representing *A. boisei*, *A. africanus* and *H. erectus*, the early *Homo* fossils do not consistently cluster together, or show the closest affinities with one another. Instead they show affinities to other hominids and different taxa. This also suggests that there was more than one species of gracile hominid in Plio-Pleistocene East Africa.

With respect to the vault KNM-ER 1470 most closely resembles the two *Homo erectus* crania, KNM-ER 3733 and 3883, or it occupies an intermediate position between KNM-ER 3733 and 3883 and the smaller earlier *Homo* specimens and the australopithecines. KNM-ER 1813 and OH 24 are more similar to the australopithecines, whereas KNM-ER 1805 is not especially close to any other hominid.

The face of KNM-ER 1470 is most similar to the robust australopithecines, particularly KNM-ER 406, whereas KNM-ER 1813 and OH 24 are closest to one another and to the gracile australopithecine, Sts 5. The fact that the multivariate phenetic comparisons show that KNM-ER 1470 is similar to KNM-ER 406 is hardly surprising. As discussed in Chapter 4, the large, broad and orthognathic face of KNM-ER 1470 is very robust australopithecine-like in some respects. The phenetic resemblances of KNM-ER 1813 and OH 24 to Sts 5 are also not surprising; many authors have identified similarities between KNM-ER 1813, OH 24 and gracile australopithecines (Anonymous, 1972; Bilsborough and Wood, 1988; Franciscus and Trinkaus 1988; Olson, 1978; Wolpoff, 1994).

What is significant about these phenetic comparisons is not that the early *Homo* specimens resemble australopithecines, but rather that the larger and smaller specimens show affinities with different taxa rather than with one another. This is difficult to reconcile with the argument that they all belong to the same species. In addition it resurrects a rather interesting possibility that has received little consideration recently: it may the case that KNM-ER 1813 and OH 24 represent *Australopithecus* rather than *Homo*.

The results of the multivariate analyses strongly suggest that there is probably more than one species of gracile hominid in East Africa during the Plio-Pleistocene, they do not demonstrate that there are only two species. Groves (1989) identified three species of early *Homo*, and Groves and Mazák (1975) suggested that there could be four. The results of the multivariate comparisons with the modern hominoids and the fossil hominids, the phenetic distances between KNM-ER 1470, 1805, 1813 and OH 24, and the distances between

these specimens and the other Plio-Pleistocene hominids, can be combined to provide a framework for a tentative sorting of the early *Homo* fossils. It must be borne in mind of course that this is based entirely on phenetic resemblances and differences.

Beginning with the two most complete, and also the most disparate specimens, KNM-ER 1470 and 1813, the comparisons with the modern hominoids and the fossil hominids demonstrate that these two are unlikely to represent the same species. Even if *Homo habilis* were as sexually dimorphic as modern gorillas the size differences in the face and vault of KNM-ER 1470 and 1813 are so large that the probability that they could both belong to *Homo habilis* is small. It is much more likely that KNM-ER 1470 and 1813 represent different species.

The multivariate comparisons between KNM-ER 1470 and OH 24 show that these two are also unlikely to belong to the same species, although the differences between them are not as large as the differences between KNM-ER 1470 and 1813. In the vault the resemblance between KNM-ER 1813 and OH 24 is not particularly strong, although the differences are not large enough to warrant placing them in different species. The Mahalanobis and shape distances between KNM-ER 1813 and OH 24 are well below the upper 95th percentiles for all of the modern reference groups (Tables 19 and 21, pp. 185 and 187). In the face however, the two are much more similar to one another than either is to any other hominid and therefore they can be reasonably assigned to the same species.

Finally, there is KNM-ER 1805, a specimen which has been described as 'enigmatic', 'bizarre', and a 'taxonomic nightmare' (Leakey, 1974; White et al., 1981; Wolpoff, 1996; Wood, 1993). The multivariate comparisons with the modern hominoids indicate that, like KNM-ER 1813 and OH 24, KNM-ER 1805 is unlikely to belong to the same species as KNM-ER 1470. However, the Mahalanobis and shape distances between KNM-ER 1805 and 1813 are much larger than the distances between KNM-ER 1470 and 1813, or between KNM-ER 1470 and 1805 (Tables 32 and 34, pp. 212 and 214). The Mahalanobis and shape

distances between KNM-ER 1805 and 1813 are so large that they exceed the upper 99th percentiles for *Pan*, *Pongo* and modern *Homo* (Tables 33 and 35, pp. 212 and 215). The probability that KNM-ER 1805 and 1813 are conspecific is even smaller than the probability that KNM-ER 1805 belongs to the same species as KNM-ER 1470. This would seem to suggest that KNM-ER 1805 represents a third species of gracile hominid. This conclusion is supported by the fact that KNM-ER 1805 exhibits a peculiar combination of features that is not found in any recognized hominid species. However, it may be the case that the singular morphology of KNM-ER 1805 is the result of abnormal growth (Kimbel et al., 1981; Thompson, 1992). While this might seem to be a case of special pleading, Thompson (1992) has shown that there are certain unusual features in the cranial base of KNM-ER 1805 that are not seen in any extant hominoid or in any other fossil hominid and which seem to indicate an aberrant pattern of growth.

CHAPTER 11

SUMMARY AND CONCLUSIONS

Early *Homo*: How many species?

Sir Wilfrid Le Gros Clark's opinion of *Homo habilis* could not have been any less prophetic. It may be that in his opinion *Homo habilis* did not deserve to be the subject of a prolonged controversy, but paleoanthropologists have been arguing about the integrity of this taxon for more than 30 years. In this dissertation I have attempted to resolve this controversy by using randomization methods and univariate and multivariate statistics to compare dental and craniometric variation in early *Homo* with variation in modern hominoids and fossil hominids. The results of these analyses strongly suggest that there is more than one species of early *Homo*. This conclusion is supported by several lines of evidence: the large degree of relative variation in the early *Homo* dental sample; the size differences between KNM-ER 1470 and the smaller early *Homo* crania, KNM-ER 1805, 1813 and OH 24 which are large even when compared to the size differences seen in the most dimorphic apes; and the phenetic comparisons of these crania with other Plio-Pleistocene hominids which show that the early *Homo* specimens do not form a coherent cluster.

The univariate analyses of dental variation show that for early *Homo* the variance in the width of P_4 is significantly greater than the variances in the three reference species, *Pan*, *Gorilla* or *A. robustus*. Furthermore, for the width of M^2 and M^3 the variance in early *Homo* is significantly greater than the variances in *Pan* or *A. robustus*. This indicates that in the postcanine teeth attributed to early *Homo* there is more variation in the width of some teeth than is reasonable for a single hominoid species. The pattern of dental variation in early *Homo* also appears to be unlike the pattern of dental variation in the reference samples, and this also suggests that more than one species is represented in the early *Homo* dental sample.

The strongest evidence of multiple species comes from the multivariate comparisons of the largest cranium attributed to *Homo habilis*, KNM-ER 1470, with the smaller crania that have been referred to this species, KNM-ER 1805, 1813 and OH 24. Comparisons of the size and shape differences between these specimens with the size and shape differences between individuals in modern hominoids show that the size differences, and in some cases the shape differences, between KNM-ER 1470 and the smaller crania are so large that they are unlikely to be conspecific. The size differences between KNM-ER 1470 and the smaller crania are large even when compared with the size differences found between gorillas. Thus, it is unlikely that KNM-ER 1470, 1805, 1813 and OH 24 could all belong to *Homo habilis*, unless *Homo habilis* were more sexually dimorphic than modern gorillas. The multivariate comparisons with the modern hominoids also show that there is more shape variation in the early *Homo* cranial sample than is reasonable for a single hominoid species. In addition, multivariate comparisons with other Plio-Pleistocene fossil hominids show that the size differences between KNM-ER 1470 and the smaller crania are very large when compared to the size differences between fossil hominids that are generally regarded as conspecific, and they are sometimes quite large when compared to the size differences between fossil hominids that represent different species and different genera.

Phenetic comparisons of KNM-ER 1470, 1805, 1813 and OH 24 with other Plio-Pleistocene hominids representing *A. boisei*, *A. africanus* and *Homo erectus* also suggest that there is taxonomic heterogeneity in the early *Homo* cranial sample. In these comparisons the early *Homo* specimens do not consistently cluster with one another, but rather they show their strongest affinities with different taxa. The vault of KNM-ER 1470 most closely resembles *Homo erectus* (KNM-ER 3733 and 3883) whereas KNM-ER 1813 and OH 24 are more similar to the australopithecines, and KNM-ER 1805 does not show a strong resemblance to any other hominid. With respect to the face KNM-ER 1470 is most similar to *A.*

boisei, and KNM-ER 1813 and OH 24 are most similar to one another and to Sts 5, a gracile australopithecine.

The univariate dental comparisons, the multivariate comparisons of KNM-ER 1470 and KNM-ER 1813, 1805 and OH 24, and the phenetic comparisons with other Plio-Pleistocene hominids all point to the same conclusion: more than one species is represented in the collection of fossils that have been attributed to *Homo habilis*. The phenetic resemblances between KNM-ER 1813 and OH 24 and the australopithecines hint at the possibility that these two hominids may belong in the genus *Australopithecus* rather than *Homo*. Thus, it may be the case that there really is only one species of early *Homo*, but the results of this research show that there were at least two independent lineages of gracile hominids in East Africa during the late Pliocene and early Pleistocene.

Conclusion

This dissertation began with a lengthy discussion of the epistemological and practical problems of species recognition in paleoanthropology. If there is only one message in Chapter 2 it is probably that for paleoanthropologists the issue of species recognition is a frustratingly difficult problem. Unfortunately, it is also a persistent problem because we are constantly faced with the difficult task of determining whether the variation that we see in our collections of fossils is intra- or interspecific in nature. Even without the epistemological difficulties species recognition is a vexing problem because we are inevitably forced to work with samples that are very small, sometimes as small as two, because our samples are incomplete and fragmentary, and because there are few appropriate methods that can be used to evaluate hypotheses about variation in an objective or rigorous way.

It would be nice if we could somehow solve the problem of species recognition, or perhaps get around it, get over it, or at least not have to worry about it so much. It is however, an important problem and we ought to worry about it. If the purpose of paleoanthropology is to reconstruct human evolution, and if species are the units of evolu-

tion or the units within which evolution occurs the problem of species recognition cannot be avoided nor can it be ignored. In this dissertation I have not attempted to answer any of the 'big' questions about fossil species. That is far beyond my abilities. My concern has only been with the more practical issues of recognizing and identifying fossil species. The computer intensive statistical methods developed and used in this dissertation can be used to answer questions about variation in fossils in an objective and statistically sound manner, even when samples are small and fragmentary. In particular the use of multivariate statistics and randomization is a methodology that has enormous potential for resolving questions about taxonomic heterogeneity in collections of fossils. Univariate measures of variation, such as the CV, measure only the magnitude of variation, but multivariate statistics reflect both magnitude (size) and pattern (shape) and it is even possible to evaluate differences in the degree of variation separately from differences in the pattern of variation. The randomization methods make it possible to determine the significance of the multivariate differences between fossils, and allow us to answer questions about variation in terms of probabilities. This is demonstrated by the multivariate comparisons of the differences between KNM-ER 1470 and KNM-ER 1813, 1805 and OH 24 which show that all of these fossils could represent the same species. It is not impossible. It is however, improbable.

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APPENDIX

Variable (Abbreviation, Wood's number, instrument) Definition

SC = spreading caliper
T = tape measure
DC = digital calipers

measurements taken with spreading calipers or tape measure were recorded to the nearest millimeter, measurements taken with the digital calipers were recorded to the nearest tenth of a millimeter.

Glabella-Opisthocranion Length (GOL, **1**, SC): The chord distance between glabella and opisthocranion.

Glabella-Bregma Chord (GBC, **17**, DC): The chord distance between glabella and bregma.

Glabella-Bregma Arc (GBA, **18**, T): The arc length between glabella and bregma.

Parietal Chord (PAC, **25**, DC): The chord distance of the sagittal border of the parietals, from bregma to lambda.

Parietal Arc (PAA, **26**, T): The arc length of the sagittal border of the parietals, from bregma to lambda.

Bregma-Sphenion Chord (BSC, **21**, DC): The chord distance between bregma and sphenion. Sphenion is identified as the point where the coronal suture meets the squamosal suture (for apes) or where the coronal suture meets the suture between the parietal and sphenoid (for humans).

Sphenion-Asterion Chord (SPC, **27**, DC): The chord distance along the temporal border of the parietal, from sphenion to asterion.

Lambda-Asterion Chord (LAC, **31**, DC): The chord distance along the lambdoid border of the parietal, from lambda to asterion.

Asterionic Breadth (ASB, **14**, DC): The chord distance between left and right asterion.

Minimum Frontal Breadth (MFB, **8**, DC): The minimum chord distance between left and right frontotemporale. Frontotemporale is defined as the point on the frontal at which the distance between the superior temporal lines is at its minimum.

Maximum Cranial Breadth (XCB, **9** or **10**, SC): The breadth across the parietals or temporal squamae at the site of maximum breadth.

Porion-Porion Breadth (POB, **11**, SC): The chord distance between left and right porion. Porion is defined as the point on the upper margin of the external auditory meatus which is vertically directly above the center of the meatus.

Bijugal Breadth (JUB, **51**, DC): The chord distance between left and right jugale. Jugale is defined as the point on the zygomatic at which the uppermost edge of the temporal process and the posterior edge of the frontal process meet.

Superior Facial Breadth (FMB, **49**, DC): The chord distance beteen left and right fronto-malare temporale. Frontomalare temporale is the most lateral point on the zygomaticofrontal suture.

Biorbital Breadth (EKB, **50**, DC): The chord distance between left and right ektoconchion. Ektoconchion is defined as the intersection of the lateral border of the orbit with a line bisecting the horizontal axis of the orbit.

Orbital Breadth (OBB, **56**, DC): The chord distance between ektoconchion and maxillo-frontale. Maxillofrontale is defined as the point where the lacrimal crest crosses the maxillofronal suture.

Orbital Height (OBH, **57**, DC): The chord distance between the superior and inferior orbital margins perpindicular to the chord that measures orbital breadth. This is an inside measurement.

Interorbital breadth (IOB, **55**, DC): The chord distance between left and right maxillo-frontale.

Nasal Breadth (NLB, **68**, DC): The maximum width of the anterior nasal aperture. This is not an inside measurement.

Nasal Height (NLH, **69**, DC): The chord distance between nasospinale and nasion. Nasospinale is defined as the point where a line tangent to the curves of the lower border of the nasal aperture crosses the median plane.

Nasion-Prosthion Height (NPH, **43**, DC): The chord distance between nasion and prosthion.

Minimum Malar Height (MMH, **59**, DC): The minimum chord distance between the inferior margin of the orbit and the inferior border of the zygomatic, medial to the origin of the masseter.

Maxillo-Alveolar Breadth (MAB, **88**, DC): The minimum chord distance between the outer surface of the alveolar processes at the midpoint of the upper second molars.

Intercanine Breadth (CCB, **98**, DC): The minimum chord distance between the alveoli of the upper canines.

Palate Breadth (PLB, **91**, DC): The chord distance between the inner aspect of the alveolar process at the midpoint of the second upper molar.

P3 - P4 Alveolar Length (PMA, **96**, DC): The minimum chord distance between the alveolar septa between P3/C and P4/M1.

VITA

Steven Mark Donnelly was born in Omaha Nebraska on July 23, 1960. Following a relatively uneventful childhood and adolescence he attended the University of Nebraska at Omaha in 1978 where he majored in psychology. Two years later, after developing a strong interest in biology and science, he transferred to Nebraska Wesleyan University in Lincoln Nebraska. There he studied biology and psychology and in 1983 he graduated with a Bachelor of Science degree in Biopsychology. In 1986 he entered the University of Tennessee, Knoxville as a graduate student in the department of anthropology. In May, 1990 he received a Master of Arts degree in Anthropology and in May, 1996 he received a Doctor of Philosophy Degree in Anthropology with a minor in Statistics. His primary research interests are in the areas of hominid evolution, evolutionary theory, statistics and morphometrics and the history of physical anthropology.

Dr. Donnelly is married and has four children. His interests and hobbies are reading, cooking, riding his bicycle and taking care of and playing with his children. He is very proud of the fact that he is able to complete the New York Time Sunday Crossword, in ink, about half the time. He also has more Legos than any other adult that he knows of.