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A REASSESSMENT OF THE TAXONOMY AND DEFINING CHARACTERISTICS OF THE GENUS *Australopithecus* AND ITS CONSTITUENT SPECIES AS DETERMINED BY OUTGROUP COMPARISON

By

Darryl James deRuiter

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MASTER OF ARTS

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Abstract

Traits and measures which were used in the past to define fossil hominid species were repeated on extant primates to determine if they were capable of distinguishing these primates statistically.

Functional definitions of the terms species and genus were derived to allow for analysis, and it was determined that only morphological features could be utilized to study paleontological materials.

The results of this study indicate that there has been a significant amount of taxonomic overclassification in the past. After analyzing the validity of the many traits used to define hominid fossil species, it was concluded that only *Australopithecus africanus* was a valid 'gracile' hominid species, excluding *A. afarensis*. For the 'robust' australopithecines, it was noted that the claims for the re-erection of the genus *Paranthropus* were supported by this study. Included within this genus were also three species, *P. aethiopicus* (represented by KNM-WT17000), *P. robustus*, and *P. boisei*.

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I would like to thank my advisor, Dr. William Wade, for all his advice, support, and criticism, without which this work would not have been possible, or even legible. His patience and dedication comprise a significant portion of this study. The effort he put into reviewing this work, and into preventing me from making any major scientific blunders, is truly appreciated. I would also like to thank Dr. Jeff McKee and Dr. Lee Berger of the University of the Witwatersrand for their advice and help in the formulation of this research design. Thanks must also go to Professor Phillip V. Tobias for inviting me to South Africa to view first hand the wonderful fossil collection at Wits University, and for inspiring such interest in the subject of palaeo-anthropology.

I wish to express my gratitude towards Dr. Bruce Latimer of the Cleveland Museum of Natural History for granting me access to the wonderful collections of primate materials in his care, as well as discussion regarding the nature of the hominid fossil record. As well, I would like to thank Dr. Ross MacPhee of the American Museum of Natural History and Dr. Richard Thorington of the National Museum of Natural History for allowing me to study the extensive collections in their care.

Thanks as well go to my thesis examining committee who did an exemplary job reviewing this admittedly long-winded and dry thesis. Their patience in reading 700+ pages is truly remarkable.

Finally, I would like to thank Brett Waddell for many inspiring discussions regarding my "dead monkeys." His frank and cogent criticisms served to continually bring me back to reality, forcing me to rethink many of my ideas and presuppositions. His input will be sadly missed. It is to his memory that this thesis is dedicated.

Although the above mentioned persons contributed significantly to the content of this thesis, any and all errors made are the sole responsibilty of the author.

List of Tables

List of Abbreviations

Myr	Million years ago	dating of geologic events
etc.	et cetera	and so forth
e.g.	exempli gratia	for example
i.e.	id est	that is (to say)
cf.	confer	compare (closest to)
et al.	et alii	and others
spp.	species	
spp. indet.	species indeterminate	
ICZN	International Code of Zoological Nomenclature	

Chapter 1 - Background

1.1 Introduction

The field of human paleontology has been characterized, since its very inception, by controversy, perhaps more so than any other area of paleontology. It is a field dominated by a small number of highly visible personalities who are often at great odds with each other. Their disagreements often move into the public arena, further enhancing the visibility of the antagonists, and to some extent the study of human evolution. It is perhaps due to our close link to our australopithecine ancestors that we have such an intense interest in their study, and that they hold such public fascination. New finds make headlines even today, and the naming of a new species is still popularly received in newspapers and on television.

Much of the controversy surrounding the early hominids revolves around taxonomy. Just how many species of hominids existed in the Pliocene and Pleistocene, and how do we differentiate them, are questions that have plagued human paleontology since the late 1930's when Robert Broom was making his many discoveries in South Africa. This debate rages unabated today, and in fact, it will be shown that it has increased in magnitude and complexity, owing to the many new fossil finds being made currently in both East and South Africa. Rather than clarifying the taxonomy as was hoped, the improvements in the fossil record have only served to provide us with an ever more confusing picture.

It is understood that the study of palaeo-anthropology extends farther than just the australopithecines, into our own genus, *Homo*. However, the complicated history of *Homo* is beyond the scope of this study. In the past, no fewer than 22 genera and 54 species (possibly more) have been postulated as having been separate taxa in numerous combinations, though today all are included within the three commonly accepted species of *Homo* (Szalay and Delson, 1979). This confused picture has been resolved to some extent by other researchers. The main problem still existing today is the actual phyletic relationship between *Homo* and *Australopithecus*. Since most authors accept the two as representing a phyletic lineage, is the generic distinction warranted? This question cannot be answered by the present study, but does present an interesting avenue for future research. Most believe that the differences between the two genera are in fact sufficient, but not all accept this view (e.g., Robinson, 1954, 1972a,b).

The Genus Australopithecus

The genus *Australopithecus* was for years typically accepted as containing the following species:

- *A. africanus*
- *A. robustus*
- *A. boisei*

based on Tobias (1967b) wherein he formally defined these as the species of *Australopithecus* and discounted all others, including the genera

Paranthropus and *Zinjanthropus*. In spite of his work, there are today numerous authors (e.g., Clarke, 1976, 1985; Grine, 1981, 1985, 1988a,b; Olson, 1981, 1985; Robinson, 1962, 1965, 1972; Susman, 1988; Wood and Chamberlain, 1987) who still prefer to use the genus *Paranthropus* for the "robust" species:

P. robustus
P. boisei

In 1978, the latest australopithecine species to be described, *Australopithecus afarensis* was proposed by Johanson, et al. Today *A. afarensis* has achieved widespread, though by no means complete, acceptance. Therefore, the constitution of the genus *Australopithecus* is usually represented as:

A. africanus
A. robustus
A. boisei
A. afarensis

Quite often in the past, new genera and species have been named on the basis of insufficient data, and by a questionable use of the generic or specific distinction. Many of these hominid genera have been subsequently placed within extant genera [e.g., *Homo* (Mayr, 1950; Brace and Montague, 1965; Wolpoff, 1975), *Meganthropus* (Weinert, 1950) into *Homo*, *Paranthropus* (Broom, 1938) into *Australopithecus*, *Paraustralopithecus* (Arambourg and Coppens, 1967) into *Australopithecus*, *Plesianthropus* (Broom, 1938) into *Australopithecus*, *Präanthropus* (Hennig, 1948) into *Australopithecus*, *Telanthropus* (Broom and Robinson, 1949) into *Homo*, *Zinjanthropus* (Leakey, 1959) into *Australopithecus*], and proposed species have often been referred to existing species.

To obtain a brief glimpse at the disparate nature of australopithecine taxonomy, the following is a list of genera and species that have in the past been put forward, but today are subsumed within the four generally accepted species of the genus *Australopithecus* (based in part on Szalay and Delson, 1979). It is recognized that not all researchers will accept this view, but it is the most commonly held one, and it is after all the purpose of this study to determine the taxonomic standing of the australopithecines. These are the taxa that the author was able to locate:

Australopithecus africanus (Dart, 1925)
Australopithecus transvaalensis (Broom, 1936)
Plesianthropus transvaalensis (Broom, 1938)
Paranthropus robustus (Broom, 1938)
Australopithecus (Paranthropus) robustus (Broom, 1938)
Africanthropus njarasensis (Weinert, 1939)
Australopithecus prometheus (Dart, 1948)
Australanthropus africanus (Heberer, 1948)
Präanthropus spp. (Hennig, 1948)
Praeanthropus africanus (Senyürek, 1955)
Paranthropus crassidens (Broom, 1949)
Telanthropus capensis (Broom and Robinson, 1949)
Meganthropus africanus (Weinert, 1950)
Homo transvaalensis (Mayr, 1950)
Hemianthropus peii (von Koenigsvald, 1957)
Zinjanthropus boisei (Leakey, 1959)

Australopithecus (Zinjanthropus) boisei (Leakey, Tobias, and Napier, 1964)

Tchadanthropus uxoris (Coppens, 1965)

Australopithecus (Australopithecus) africanus (Howell, 1965)

Homo africanus (Brace and Montague, 1965, in part, *nec* Weidenreich, 1928)

Australopithecus boisei (Tobias, 1967)

Australopithecus (Paranthropus) robustus (Howell, 1967)

Paraustralopithecus aethiopicus (Arambourg and Coppens, 1967)

Australopithecus robustus (Howell, 1969, in part)

Homo robustus (Wolpoff, 1971b)

Australopithecus africanus (Campbell, 1972, in part)

Australopithecus crassidens (Howell and Coppens, 1976)

Australopithecus aff. africanus(Howell and Coppens, 1976)

Australopithecus afarensis (Johanson, White, & Coppens, 1978)

Australopithecus (Paranthropus) aethiopicus (Kimbel, White, and Johanson, 1988)

Ardipithecus ramidus (White, Suwa and Asfaw, 1995)

Australopithecus anamensis (M. E. Leakey, 1995)

We can see from this list that there have in the past been 15 genera and 14 species names used in at least 30 combinations. There has obviously been a great deal of shifting around of specific and generic names in the past, a practice that continues today. Some of the species have also been officially reasserted at times. The increase in the number of newly discovered hominid fossils will eventually require firm taxonomic placement, so that resolution of this problem is increasingly necessary.

The status of *Paranthropus* is under considerable debate at the moment, with some authors accepting it as a valid taxon (Clarke, 1976, 1985; Grine, 1981, 1985, 1988a,b; Olson, 1981, 1985; Robinson, 1962, 1963, 1972a,b; Susman and Brain, 1988; Susman, 1988; Wood and Chamberlain, 1987). Most palaeo-anthropologists still prefer to place the robust lineage within *Australopithecus*, but the number of authors accepting *Paranthropus* is growing. There appears to be very little discussion regarding the genus concept, and little in the way of defining characteristics. It is apparently presumed that the dietary adaptation of the "robust" australopithecines was different enough from the "gracile" members that a generic distinction is warranted.

From its initial naming, the species *A. afarensis* (Johanson et al., 1978) has been hotly disputed. Although there are numerous researchers who accept it as valid, there are many who continue to argue against it (Boaz, 1979, 1983; Day et al., 1980; Kennedy, 1980; Olson, 1981, 1985; Tobias, 1980, 1981, 1983; Wolpoff, 1983). There obviously is still a great deal of contention surrounding the taxonomy of the australopithecines. This study provides a much more comprehensive look at all the various members of the genus *Australopithecus* and their nomenclature. It will be an attempt to resolve the current debate.

A re-evaluation of the systematics and taxonomy of the late Pliocene and early Pleistocene hominids, particularly the australopithecines, appears to be necessary, in order to help accommodate all the information that is to be found in the new hominid fossils of southern and eastern Africa, as well as the already known fossils. The criteria upon which new species have been named in the past within *Australopithecus* were examined in this study to determine if they are actually sufficient to warrant a specific or generic distinction.

1.2 The Species Problem in Human Paleontology

Integral to this entire thesis is a discussion and definition of the term species. To attempt to delineate the australopithecine species without a precise understanding of the term would be to fall into the trap this study attempts to illuminate. In the past, numerous species have been defined based partly on an insufficient understanding of exactly what species are, and how they are defined. I will therefore provide a detailed discussion of what the term species means, what ideas and concepts of species have been used in the past, and what I will be using as an operational definition of species throughout this study. The most logical place to put such a pivotal discussion as this is at the very beginning of the work, so that the reader will have a full and complete understanding of what I mean when I use the word species.

The term Human Paleontology will be used throughout this study, rather than the more familiar Paleoanthropology. The reason is that, according to Howell, "paleoanthropology, broadly conceived, is concerned with investigations of the biological relationships and the evolutionary history of the Hominidae, and of the development among the Homindae of capacities and capabilities for culture (Howell, 1967:471)." This thesis will deal only with morphological features of the skeleton of australopithecines and of modern apes. No attention will paid to culture, or to genetical-biological aspects of any of the groups studied. Therefore, the term paleontology will be applied, as it holds no cultural connotations, and generally (though certainly not exclusively) deals with skeletal anatomical traits only.

1.2.1 Species - Historical Perspectives

The term species in biology has been the subject of intense debate for the past 200 years, with a vast number of different definitions being put forward by numerous different authors. For thousands of years prior, people also sought to classify the natural world around them, to order all the different varieties of flora and fauna they saw. Obviously, the separation of various groups of living organisms into groups based on some sort of similarity criteria is important to people. In the 18th century the Swedish naturalist Carolus Linneas categorized the biological organisms of the natural world into different varieties, now commonly referred to as species. In the late 19th century, Charles Darwin took this a step further and proposed the mechanism by which species change and diversify, namely, natural selection. However, in his book *On the Origin of Species* Darwin fell short of the mark by not actually looking at the multiplication of species, only their gradual evolution (Mayr, 1959b: 385; 1970:10). Over the years many different definitions of species have continued to accumulate.

Originally, the term species was ill defined, being recently borrowed from the field of geology in the mid 1800's. A species was simply anything that was different from a similar such entity, e.g., one type of rock was a different species from another rock. The biological connotations added to the term when it was first borrowed were not fully realized. A species was thought by many to be an abstraction, an arbitrary division of nature imposed by humans. Darwin himself defined species as follows:

> I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety which is given to less distinct and more fluctuating forms. . . . The amount of difference is one very important criterion for settling whether two forms should be ranked as species or variety. (Quoted in Mayr, 1959a:4)

Darwin failed to grasp a clear concept of species, and this prevented him from uncovering the processes behind speciation, from uncovering the true origin of species. Early Mendelianists also denied the existence of species as real entities. This lead C. E. Bessey to exclaim in 1908 that, "Nature produces individuals and nothing more. . . . Species have no actual existence in nature. They are mental constructs and nothing more. . . . Species have been invented in order that we may refer to a great number of individuals collectively (quoted by Mayr, 1959a:4)." Others felt that species were "a community or number of related communities whose distinctive morphological characters are in the opinion of a competent systematist sufficiently definite to entitle it or them to a specific name (Regan, 1926, quoted by Imbrie, 1959:127)."

With the work of such researchers as Ernst Mayr and Theodosius Dobzhansky in the late 1930's and early 1940's, the understanding of the term species began to shift. It was realized that species are in fact, real entities, and that they do exist in the real world. A biological definition was formulated to take into account the biological aspect that had been missing from previous formulations. Ecology, populations, and genetics were factored into discussions of species, and this in turn was assimilated into what has come to be known as the Modern Evolutionary Synthesis. Numerous definitions of species continued to proliferate, but most were simply variations on Mayr's biological theme (to be discussed below).

1.2.2 Principles Underlying Species Concepts

All species concepts and definitions that have been put forward in the past are based on three underlying theoretical concepts (Mayr, 1959:11). These are the typological concept, the non-dimensional concept, and the multi-dimensional concept. These form the basis for all other concepts which have been put forward in the past. All are derived in theory from the basic typological, non-dimensional, and multi-dimensional underpinnings. A firm understanding of these underlying principles must be achieved before a definition of species can be attempted.

The Typological Species Concept is the simplest concept, as well as the most prevalent concept, especially in history. It can be variably referred to as the morphological species concept as well. Individuals of a species are only reflections of one type, the shadows of the Greek *eidos* (Latin equivalent = *species*) (Mayr, 1959a:11). This *eidos* is constant, and variability of individuals has no effect on it. Variation, in fact, is a result of imperfect manifestation of the idea, or *eidos*, implicit in each species. Morphological similarity is therefore what defines the species concept (Mayr, 1970:11). The use of morphological differences as species criteria is very different from the use of morphological evidence. Morphological difference is not the decisive criterion, even though it is commonly (and incorrectly) used. This belief is very important to the field of human paleontology, a matter to which I shall return later. This scheme, the typological concept, cannot deal with intraspecific variation. This concept sees species as only individual organisms, not as natural populations.

The Non-Dimensional Species Concept looks at the relationship of two coexisting natural populations that are sympatric and synchronic (Mayr, 1959a:14). It possesses no dimension of time, or change through time. This concept is based on distinctiveness, not difference. This is generally the concept used by field biologists when they separate different groups of animals in the wild. It is based on the idea of reproductive isolation. Two populations that are incapable of, or unwilling to, reproduce are considered different species. A species in this idea exists only in relation to other such entities (much like the term brother only has significance in relation to another such entity). It is unfortunately unable to deal with the dimensions of space and time. Two groups of animals may be reproductively isolated due only to geographical isolation, and would readily interbreed if brought into contact. Also, and more importantly to the paleontologist, the reproductive isolation of groups of fossil animals can never be known, be it with groups of fossils from sites separated by long distances, or those separated by long geological time spans.

The Multi-Dimensional Species Concept considers species as groups of populations that actually or potentially interbreed with each other (Mayr, 1959a:16). The multidimensional species concept is the more practical of the various concepts, and is better able to deal with naturally occurring populations. In the past, systematists and taxonomists such as Mayr believed that the multidimensional concept was the closest to reality, but that it lacked scientific objectivity.

A main factor in this concept is gene flow. It is gene flow that defines members as belonging to the same species. Individuals of different species can on occasion hybridize, but the offspring are often sterile. Even if the offspring are viable, it is likely that they will be less fit for survival. Either way, the genes of the two populations are not likely to be transferred, i.e., there will be no gene flow. There can be reproduction with no gene flow, therefore different species can interbreed and still be separate species (Bock, 1986:33, 41; Mayr, 1963:551-2).

The practical application of the multi-dimensional concept is problematic and requires arbitrary decisions to be made on the specific status of particular populations (Bock, 1986:37). However, this is the practical application of the species concept in the field of biology, as opposed to the theoretical non-dimensional concept. It takes into account gene flow between populations, as well as temporal and spatial factors.

1.2.3 The Biological Species Concept

Today, most biologists would agree on a definition of species put forward by Ernst Mayr in 1942 which states, "*species are groups of actually or potentially interbreeding populations in nature which are reproductively isolated from other such groups..*" This definition draws heavily upon the non-dimensional view, and is in fact a direct derivative of it. The basic difference between species is reproductive isolation. It is in the flowing of genes that the multi-dimensional species concept makes its contribution to its derivative biological species concept. However, the time frame that this gene flow adds is still not sufficient to deal with the huge expanses of time that paleontologists must deal with.

There are three main aspects of the biological species concept. First, species are defined by distinctiveness rather than difference. This looks at not just how species differ from each other in certain features, but what actually sets species apart from each other, what makes them unique. Second, species consist of populations instead of unconnected individuals. The existence of populations was often ignored, especially in paleontology, where the fossils themselves were named, with little consideration of the fact that these fossils once belonged to distinct, living, breathing, reproducing, natural populations, precisely like those that exist today. Third, the decisive criterion is not fertility, but reproductive isolation of populations. That certain animals of different species *could* potentially reproduce was accepted (albeit, usually with reduced viability of the offspring); however, in most situations this interspecific breeding *would not* occur. The animals would not recognize each other as potential mates for various reasons discussed below.

Recently it has been noted that many biologists have not made notice of the distinction between reproductive isolation and genetic isolation (Bock, 1986:34). Reproductive isolation means only that no gene flow exists between different species, not that they cannot interbreed and produce hybrids (i.e., not that said gene flow cannot happen). Bock has therefore proposed a new definition of species, namely that, "*a species is a group of actually or potentially interbreeding populations of organisms which are genetically isolated in nature from other such groups* " (Bock, 1986:32). This means that it is the lack of gene flow, not lack of reproduction that defines a species.

Species, it must be noted, make up a reproductive community. The concept of reproductive isolation that Mayr and many others use relies on the isolation of two populations. This isolation can come in the form of pre-mating or post-mating mechanisms (Mayr, 1963:57). Post-mating mechanisms involve such aspects as infertility, hybrid inferiority, and hybrid sterility.

Pre-mating mechanisms are those which serve to prevent mating between different species from occurring. There are two main concepts here that determine whether or not mating occurs; potential mates do not meet, and potential mates meet but do not mate (Mayr, 1970:57). Mates do not meet because of such factors as habitat isolation and seasonal isolation. Habitat isolation simply means that two groups are sufficiently far enough apart that they will not meet. The problem with this is, and Mayr notes this as well, that when the habitat isolation breaks down, hybridization occurs. This is a rather troublesome point, in that the simple fact of distance is used to make species boundaries. This is an arbitrary distinction, and the fact that some animals are far enough away that they don't reproduce takes precedence over the fact that they actually can reproduce.

Another factor is that habitat isolation and seasonal isolation are not effective mechanisms in highly mobile animals, such as hominids. We can see that among human populations, even though they do not meet through geographic isolation, they are still considered to be conspecific. A more objective distinction is definitely needed. With regard to seasonal isolation, differences in the breeding season can prevent interbreeding. Mayr admitted that the actual contribution of seasonal isolation is largely unknown (Mayr, 1970:58), and this concept seems to be most commonly applied to insects and water dwelling animals such as fish.

The second set of pre-mating mechanisms are ethological, or behavioral, barriers. To Mayr this was the largest and most important isolating mechanism (Mayr, 1969:316). Incompatibilities in behavior between species constitutes an effective barrier. Particular regard is given to courtship rituals that males and females of different species exhibit in order to attract mates. Visual stimuli, such as bright coloring etc., are considered, but these factors have limited utility with regard to hominids, and the same can be said for auditory stimuli (both appear to have the most utility for insects and birds).

Behavior is the most important factor. Males of a species will engage in some sort of courting activity until they receive stimuli from a potential female mate that copulation can begin. If this return stimuli is not presented, mating will not occur. Two different species are thought to display different mating behaviors, so that mating will not occur between two different species since there is a lack of the proper stimulus and response necessary (Mayr, 1970:62). In Mayr's view, behavioral differences occur to prevent hybridization between closely related species.

1.2.4 The Evolutionary Species Concept

Although the biological species concept is the most widely accepted species concept today, it is by no means the only one. Many have sought to answer one of the major failings of this concept, its inability to deal with fossil lineages. In 1961, George Gaylord Simpson introduced his Evolutionary Species Concept. The intent of this concept was to be able to deal with paleontological species as well as neontological species. Simpson stated that, "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies (Simpson, 1961: 153)."

It was later modified by Wiley to read that, "A species is 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 (1978:18)."

This new species definition essentially gave time depth to the idea of species. A problem inherent to this idea was noted originally by Simpson in that if you begin with a species, it can be traced back through time all the way to the beginning of life on this planet. Simpson avoided this regression in classification by stating that paleontologists must subdivide evolutionary species into arbitrary temporal species. This was what in essence was already being done by most paleontologists, and the new species concept attempted to codify this practice. Many rejected this idea of necessary arbitrary divisions, and the concept was not widely adopted.

In 1978, Wiley attempted to revive the evolutionary species concept, this time using the new idea of punctuated equilibrium to divide species. Punctuated equilibrium, in its simplest form, states that species throughout evolutionary history undergo long periods of stasis, where little evolutionary change takes place (the equilibrium). Then, at certain critical points, rapid evolutionary change takes place, usually as a result of a shift in environment, or the reproductive isolation of a small descendant population (the punctuation - for a much better discussion of punctuated equilibrium, please refer to Eldredge and Gould, 1972). This idea is essentially a paleontological view of Ernst Mayr's allopatric speciation model, whereby a daughter population becomes separated from the larger parent population and undergoes differential evolutionary change, due to its reproductive (geographic) isolation. When the two species are again able to contact each other, they are no longer able (or willing) to mate with each other (Mayr, 1982:1122).

This species concept, in spite of its subsequent reformulation, is still laden with difficulties, not the least of which is the fact that many researchers do not accept the theory of punctuated equilibrium to be valid (see Gingerich, 1984, for a critical review of punctuated equilibrium). That removed, the necessity of arbitrary species distinctions seems to remove the necessity for this new concept, as this practice is already widespread. In spite of its attempt to reconcile species and paleontology, this concept has not received wide acceptance.

1.2.5 The Competitive Species Concept

This concept was put forward in 1975 by Michael Ghiselin as a radical solution to the species problem (although he gave his idea no name - I have named it such in my all too human need to classify). Ghiselin defined species as "the most extensive units in the natural economy such that *reproductive competition* occurs among their parts (Ghiselin, 1975:538 italics mine)." The key factor for Ghiselin was not morphological or genetical similarity but, rather, mode of competition. He believed species to be individuals rather than collections of organisms. Species names were proper names and, as such, no name could be taken to imply the activity of the individual. The potential interbreeding of species no longer mattered, as it is of little importance whether an individual is interbreeding at any given moment. All members of a species are competing reproductively with all others (Ghiselin, 1975:538). Species do not have defining properties, and their constituent organisms are parts of the greater individual.

Essentially what Ghiselin was looking at was defining species based on their reproductive competition. Organisms that competed with each other for reproductive activities would be considered conspecific. It matters little what other species are doing in relation to each other, as the definition in this case is *internal* to the group. I am considered an individual entity, even though I am composed of numerous different biological systems, or dividing even further, trillions of separate cells. I function as an integrated system, regardless of what my numerous internal divisions are doing. The same was held for species. The actions of organisms simply went towards making up the corporate whole, the species. The species as an individual has no defining characteristics for its parts (my heart and my liver are two entirely different and non-comparable organs, yet they are still part of the greater whole). Morphology and genetics were no longer relevant, only reproductive competition.

On a philosophical level, this concept makes sense, and many agreed with its tenets, but actual application became difficult. Ghiselin provided no mechanism for implementing his ideas, or any indication of how to go about renaming all known animal species. It is one thing to define a concept, but quite another to go out and define the reproductive competition required by this concept. Beyond this, and more germain to this discussion, is the fact that this concept falls quite short of providing a solution for paleontology.

The reproductive competition of extinct species will likely never be known. The ecological niche of fossil species can only be guessed at in a very incomplete way. We will never be able to know all that would be required to utilize this concept in paleontology, and it is here that this concept becomes untenable.

1.2.6 The Species Problem in Human Paleontology

Rather than looking at variable interbreeding populations, human paleontologists are normally only able to consider morphological differences between fossil specimens. The biological species concept is difficult to apply to fossil representatives about which we have little information on behavior patterns (Kimbel, 1991:361). Therefore, in human paleontology, in order to demonstrate consistency in the fossil record, we must look primarily at morphological characteristics, and we must make our determinations based on these similarities without information on the reproductive isolation that may or may not have existed. We are essentially left with only a morphological concept for which we can have little information on the reproductive behaviors or the population gene pool of the organisms. The separation of genera is even more difficult because a genus is arbitrarily stated by some as being a radical difference in econiche, while others consider it to be a significant morphological difference. Since species are difficult to define objectively, the problem for genera is even more pronounced.

Certain aspects of the biological species concept can still be applied, however. Human paleontologists must remember that the fossils with which they deal belonged to populations; they were not isolated individuals. As well, the variability inherent in all species today, especially the primates, must be considered when analyzing the differences and similarities between the various fossils that are being studied. In the past, variability of a population was often not recognized, and new generic and specific names were given to almost all new finds. As the hominid fossil record grew in size, the amount of recognized variability within the australopithecines was extended so that most researchers accept that all individuals now fit within the genus (sometimes genera) and a small number of species of australopithecines.

In the field of paleontology (including human paleontology), the problem of the recognition of species is particularily accute. With precious little evidence regarding the behavioral aspects of the various species being studied, the biological species concept appears to be of limited applicability. However, many believe that all is not lost, and that this concept does have something to offer the paleontologist (Imbrie, 1959:126; Mayr, 1970:19). Accepting that most fossil specimens are assigned to species based on morphological criteria, Mayr noted that most interpretations of the fossil material involve detailed use of ecological parameters such as, population dynamics and econiche (Mayr, 1959b:384).

There are numerous other authors who also accept the use of morphological criteria for the delineation of species. In spite of the insistence of the biological species concept upon reproductive isolation (a factor that can never be unequivocally determined in fossil species), and the ignorance of morpholgical criteria, Löve has stated that, "[the] discovery [of the breakdown of morphological distinctiveness when subspecies hybridize] may seem to explain the futility of using morphological characters as a basis for definitions of species; but when such traits have become fixed by reproductive isolation and changed or added to by further evolution, they become most useful tools in distinguishing the genetically closed systems

(Löve, 1964:35)." Essentially, after speciation has occurred, be it through cladogenesis or even anagenesis, the morphological distinctiveness that develops in each species can be used to define said species.

Imbrie defined the species that paleontologists must work with as *transient species*, which is a correlate of Mayr's non-dimensional species. Through various biases in the fossil record, paleontologists are able to look only at slices in the evolutionary history of a given species, usually from an isolated locality, creating these transient species (Imbrie, 1959:131). Often, however, enough fossils can be obtained to show gradual morphological change in a series of fossils, and it is in this aspect that, again, morphology plays a distinct and important role. Morphological evidence is the single most important criterion in the determination of species in the fossil record. It is the principle evidence of the primacy of evolution in the explanation of the diversity of life (Gingerich, 1985:28).

In their recent discussion of evolution and species discrimination in the fossil record, Rose and Bown (1986) came to the conclusion that gradual phyletic change ruled the day, and that punctuated equilibrium, with long periods of stasis (little evolutionary change) and events of rapid evolutionary change (punctuations) was not evident in any of the fossil species they studied. This conclusion is of great significance in the discussion of species. Their conclusion implies that species boundaries will be quite nebulous, and may have to be arbitrarily imposed (Rose and Bown, 1986: 119). As fossil records of different groups improve, the species boundaries will become increasingly obscured, and if a perfect fossil record could be found extending back millions of years, no speciation event would be detected, even though fossils sampled at different intervals might show drastic differences.

The basic point of their work was that arbitrary divisions must be imposed by the paleontologist in order to avoid such an absurd reduction. Simpson pointed out this same dilemma when he outlined his evolutionary species concept, and he came to the very same conclusion, that indeed, arbitrary species distinctions must be made. Rose and Bown went even further when they "emphasize that species considered distinct by established criteria are no less distinct if evolutionary intermediates can be demonstrated (1986:121)." This seems a difficult idea to accept, and it appears to controvert both the biological species concept and the effort of scientific enquiry. Arbitrarily defining species based on "established" criteria, with no allowance for future discoveries to make any impact seems somehow wrong, both methodologicaly and intuitively.

Despite the shortcomings of the biological species concept when applied to the fossil record, it is still of inestimable value. Morphological criteria are valid for use paleontologically, provided the interpretations of the fossil record are based on biological premises. It is therefore under this assumption of the validity of morphological criteria for species distinction that this study will be performed. Since all species and genera of early hominids (actually, all fossil species) are and were defined on the basis of their morphological characteristics, these very characteristics are equally valid for testing the specific status of the australopithecines. Species distinctions can be made comparing morphological variation of fossils. The trick then becomes how to decide exactly which morphological characteristics to use. This is the main premise of this thesis, to determine which features, traits or characteristics are actually capable of separating out hominid species in the fossil record. The pool of traits to be analyzed was gleaned from the literature available on early hominids, and it is from these traits used to define hominid species in the past that I will attempt to extract valid morphological definitions of australopithecines.

Therefore, for the purpose of this thesis, I will define a species as does Mayr: *species are groups of actually or potentially interbreeding populations in nature which are reproductively isolated from other such groups*. However, owing to the difficulties in this approach outlined above, I will add to this the idea that morphological characteristics are in fact capable of separating out these biological species. Species are groups which are reproductively isolated, but they are also morphologically distinct. The first premise of this study is that these differences in appearance will manifest themselves in numerous ways (i.e., many different traits), and can be measured and analyzed to provide us with a determination of different species. The second premise then becomes to determine exactly which traits and characteristics are valid for distinguishing between different fossil species.

1.3 The Problem and Research Objectives

In the past 70 years, since the naming of *Australopithecus africanus* by Dart in 1925, many new hominid species have been named on the basis of long lists of morphological characteristics. Little or no attention was paid to the taxonomic valency of these lists, or whether or not the traits used were in fact capable of separating out different species. An historical reassessment is required to decide which of the various australopithecine species were in fact originally based on valid criteria, and which were perhaps named using traits that are unable to distinguish between extant species.

The first step in performing this reassessment will be to review in the literature the taxonomic designation of all the species now located within the australopithecines, including *Australopithecus africanus*, *A. robustus*, *A. boisei*, and *A. afarensis*, as well as the many that have fallen by the taxonomic wayside throughout the years. Close attention will be paid to the exact characteristics utilized to define each species. A comprehensive list of all defining characteristics for each species of the australopithecines will be compiled. These traits will then be used in outgroup comparisons to determine their taxonomic validity.

As far back as 1965, the call for outgroup comparisons like those to be performed in this study went out. As Simons and Pilbeam pointed out, "in order to establish a valid species it should be necessary to show characters in the available fossil material which purport to be of the same magnitude as those which separate related living species (Simons and Pilbeam, 1965:101)." This is precisely what this study intends to do, because it is my precisely my contention that the practice outlined here has not been followed in human paleontology. Species have been named on the basis of often long trait lists, but never with an eye towards the validity of these characteristics, i.e. the ability of the traits to separate out modern species. I will therefore review the taxonomic naming of each of the australopithecine species, and determine which of the traits are capable of distinguishing between some of the closest relatives of the australopithecines, the great apes.

In an article lamenting the poor state of species discrimination in human paleontology, Ian Tattersall commented upon the seminal article of Simons and Pilbeam (a portion of which was quoted above). He felt that most anthropologists had failed to take this worthy advice, and had instead focused on intra-specific variability (Tattersall, 1986:166). Species-defining traits were usually compared to a single related species to decide if the amount of variation seen in the fossil species was greater or less than that seen in an extant species. Tattersall, however, felt that there was no consistent relationship between speciation and morphological change (Tattersall, 1986: 166). He did, at any rate, accept a certain amount of morphological generalization from living to extinct taxa.

The point of Tattersall's work, and more expressly Simons and Pilbeam's, remains that comparisons between the closest living extant taxa to the australopithecines, the great apes, must be made.

This thesis will therefore utilize the advice of Simons and Pilbeam, and look at interspecific (between-species) comparisons of traits, not at intraspecific (within-species) variation of the same traits. I will apply the traits used in the past to determine whether or not they are capable of separating out modern species. Traits used to delineate new species in the past that cannot separate out modern species will be considered insufficient for a specific distinction. This will be a test to determine if the characteristics used to name the different species of *Australopithecus* were valid, i.e., if they can distinguish between modern species.

For example, if, in the description of a new species (like *Australopithecus afarensis*), it was claimed that "presence of a diastema, strong alveolar prognathism, and third metacarpal lacking a styloid process" separated this species from all other known species of australopithecines, then these measures would be used to test whether they were capable of discriminating between species of great apes (*Pan paniscus* vs. *P. troglodytes*). If these traits were capable of distinguishing between two species of the same genus of ape, then they would be accepted as indicating a valid species. If they could not distinguish the two species, then the validity of the species they define would be questioned. Complexes of traits used to define species will be compiled and tested to determine if they in fact are capable of differentiating modern species, and whether their use for separating paleontological species is acceptable.

It must be made clear at the outset that I will not be studying the expression of traits as they are claimed for the australopithecines. It is of little importance to this particular study whether *Australopithecus africanus* has larger teeth than *Australopithecus afarensis*, or whether *Paranthropus* possesses a sagittal crest while *Australopithecus* does not. What is important is whether or not the trait itself (in any expression) will be capable of separating out two species or genera of extant apes. Can tooth size, irrespective of who possesses the larger or smaller, separate species of primates, or can the presence or absence of a morphological feature distinguish between modern taxa. Therefore, discussions of different relative expressions of traits will be ignored in favor of analysis of the taxonomic value of the trait itself.

The category "genus" has been poorly studied in the past. Most researchers accept it as an abstraction, an arbitrary lumping of species that seem to be closely related to each other. Simpson has defined a genus as:

> . . . a group of species believed to be more closely related among themselves than to any species placed in other genera. Pertinant *morphological evidence is provided when a species differs less from another in the same genus than from any in another genus.* When in fact only one species of a genus is known, that criterion is not available, and *judgement may be based on differences comparable to those between accepted genera in the same general zoological group.* (Simpson, 1963:8; italics mine)

Essentially, genera are to be considered more variable than species.

Since morphological criteria are still acceptable (again, with fossils morphological traits are almost all that is available to be studied) the difference between genera will be studied by comparison between *Pan troglodytes* and *Gorilla gorilla*. Those features unable to distinguish between the two genera of great apes will be considered invalid for a generic distinction within the australopithecines.

This being said, I realize that someone with an even moderately different definition of the arbitrary category that is the genus will be able to dispute this methodology. My only response to this can be that I am attempting to maintain internal consistency within this study. I will use the same methodology for both specific and generic distinctions. I am justified by the preceding definition of genus to use this methodology, and am confident that I am properly applying a singular scientific principle which is logically consistent. Any disagreement must be with my theoretical definition of genus, not with my scientific methodology.

1.4 The Great Ape Comparative Model

The relevant question at this point becomes, which taxa to use for my extant outgroup comparison. The answer has been alluded to above. For the specific distinctions I will be comparing *Pan troglodytes* and *P. paniscus*, and for the generic distinctions I will be comparing *P. troglodytes* and *Gorilla gorilla.*

I had considered using *Homo sapiens* as an outgroup comparison as well, but decided against it. Although modern humans are the closest living relatives to the australopithecines, their inclusion in this study would likely have skewed the results. Humans have undergone a different sort of evolution than most animals, that being evolution directed by our extreme reliance on culture and technology (not to be confused with the anthropological theory of cultural evolution).

What is meant by this is that, as a result of our all encompassing reliance on culture for survival, we have undergone changes not seen elsewhere in the natural world. For example, certain deleterious genotypes which would otherwise be selected against in nature flourish in modern populations as a result of much improved medical care.

Another example can be seen in the differential diets of human populations on this planet. In North America, most inhabitants (certainly not all) receive an optimal diet and excellent health care. In areas of Africa (for example) an optimal diet cannot be achieved, nor is there adequate health care. This factor alone can account for many of the physiological differences that are evident in skeletal populations of the two respective areas. Our reliance on culture has introduced artificial morphological differences which might well mask real interspecific variation of other primate species, and would likely produce spurious results. For these reasons (plus numerous others examples), humans have been left out of this study.

This then leaves us with the great apes as the closest living relatives of the now extinct australopithecines. Chimpanzees (*Pan troglodytes* and *P. paniscus*) have long been considered to be the closest living relatives of humans, and by logical inference, of the australopithecines. Darwin placed the origins of human evolution in Africa because the most similar morphological forms to ours were to be found there, namely the great apes. In the seminal work on primate classification, specifically within the Hominoidea, Simpson stated that, "since the 19th century it has been the usual . . . opinion that among the living mammals *Homo* is most closely related to *Pan* (Simpson, 1963:25)." He further indicated that all kinds of new evidence (including anatomical, karyological, biochemical, and behavioral) strongly supported the same conclusion. He placed *Australopithecus* in an intermediate position between *Homo* and the last common ancestor of both *Homo* and *Pan*.

As recently as 1990 this close relationship between our genus *Homo* and the great apes has been strongly supported (Goodman et al.). The split between *Homo* and its last common ancestor with *Pan* is normally placed somewhere between 4-8 million years ago (Myr), though there is strong evidence for it being as recent as 4-5 Myr (Sarich and Cronin, 1977:354; White et al., 1994:306).

Numerous different studies involving many different genetic techniques have been performed, and all support a human-chimp-gorilla clade. Of great importance here is the finding that genetic distances derived from nucleotide sequencing as well as DNA hybridization tests strongly support the phylogenetic analyses that have been constructed using morphological data (Goodman, et al., 1990:260). This would appear to be external vindication of the use of morphological criteria for the analysis of fossil and extant species of primates. Goodman et al. (1990) further found that there was significant genetical and molecular evidence that humans and chimpanzees shared a most recent common ancestor. The phyletic position of *Australopithecus* between this last common ancestor and ourselves, by inference, makes the chimpanzee the best extant taxon for comparison. I therefore will use the chimpanzee for my outgroup comparison.

The two species of chimpanzee, *Pan troglodytes* and *P. paniscus* have both been recognized as valid species since 1929 when *P. paniscus* was named by Schwarz. *Pan troglodytes* itself was named in 1779 by Blumenbach (Osman Hill, 1969:31). Numerous different specific and generic names have been proposed over the years for the genus *Pan*, but today only these two species are recognized. They are, in fact, widely recognized, and I could find no discussion arguing against these two species being separate. Most current authors accept the two as quite valid, distinct species, both morphologically and behaviorally (Chiarelli, 1968; Johanson, 1974; Kinzey, 1984; Osman Hill, 1969; Schultz, 1969; Shea, 1984; Zihlman, 1984). Chiarelli noted differences in the karyological structure of *Pan troglodytes* and *P. paniscus*, and Schultz wrote a detailed analysis of the chimpanzee skeleton wherein he noted numerous morphological differences between the two species.

The species *Gorilla gorilla* will also be used in this study, as a comparison between genera of primates. Again, a distinct human-chimp-gorilla clade is recognized (Chiarelli, 1968; Goodman, et al., 1990; Sarich and Cronin, 1977). The close relationship between the three taxa is not often disputed. However, the actual relationship between the genera *Pan* and *Gorilla* occasionally is. Most now accept humans and chimpanzees as being slightly closer phylogenetically than either is to the gorilla, though there are dissenting opinions (Andrews, 1986; Brown et al., 1982; Marks, 1983; Templeton, 1983, 1985 - all see chimpanzees and gorillas as being closer to each other than either is to humans). Some would see *Pan* and *Gorilla* as congeneric, subsumed under the genus *Pan* (Buettner-Janusch, 1963; Mayr, 1950; Simpson, 1963; Szalay and Delson, 1979). This is a minority opinion, but it does serve to illustrate the close morphological and genetical similarities seen between the two.

Owing to this extreme closeness, I have chosen *Gorilla gorilla* for my generic comparison. I feel that it is the closest other primate group to the australopithecines, and will provide the best possible contrast. An additional benefit that arises with the use of *Gorilla* is the fact that it is constantly characterized as more 'robust' than *Pan*. Since the generic distinction I am comparing it to within the australopithecines involves the "robust" vs. "gracile" hominids, this condition appears quite serendipitous. The comparability that I am seeking is further enhanced by the fact that gorillas are larger and more robust than chimpanzees. The dietary adaptations of the two ape species also seems to closely approximate the hypothesized dietary differences between the 'robust' and 'gracile' australopithecines. It is these dietary differences that lead to many of the morphological differences in the apes, and presumably the australopithecines.

Chapter 2 - Historical Analysis of Paleoanthropological Research

2.1 Introduction

The study of the australopithecines has rather a brief history, extending only as far back as 1925. It was in February of that year that the genus *Australopithecus* was born, delivered by a young Australian doctor in South Africa by the name of Raymond Dart. Dart had been able to recognize that a small fossil skull of some sort of primate infant which had been brought to him only a few months before was significantly different than anything else that had ever been seen before. It was not quite human, but neither was it a chimpanzee or gorilla. Contrary to the prevailing beliefs at the time, Dart claimed the tiny ape-like Taung Skull to be that of a human ancestor, and he named it *Australopithecus africanus*, the Southern Ape of Africa.

This claim of Dart's flew right in the face of every preconceived notion of human evolution at the time. Humans, it was claimed by such esteemed anatomists as Sir Grafton Elliot Smith and Sir Arthur Keith, had evolved their lovely large brains first, and had only later evolved the other particularily human characteristics of the teeth and skeleton. Encephalization must have preceded hominization. Proof of this idea was to be found in *Eoanthropus dawsoni*, the 'dawn man' of Piltdown in Sussex, England. The fossils belonging to this taxa clearly showed a human-like brain associated with very apelike teeth. Our brains were the primogenitor of our species.

The presence of the Piltdown remains presents two considerations in the history of human paleontology. First, they outlined exactly what the preconceptions of most eminent British scientists of the time were. The Piltdown materials are now known to have been a hoax, but for what purpose? Why go to all the trouble of artificially creating these supposed human ancestors? The most likely answer is that this was exactly what the perpetrators expected to find anyway, so they were only helping science along (Tobias, 1992:257). Men such as Keith (whom Tobias believes to be the perpetrator of the hoax; see Tobias, 1992) firmly believed that eventually this exact type of human ancestor would be found. Our enlarged brains were the first to arise, and it was these brains that defined us as separate from the rest of the natural world. Subsequent discoveries have proven the fallacy of this conception, and it is now widely held that the truly unique feature to set human evolutionary history apart from other lineages is our bipedal mode of locomotion. We have walked erect for at least 3.5 Myr, while evolving large brains only in the last approximately 2 Myr.

The second consideration that Piltdown poses is that for 28 years, until its official debunking in 1953 (Weiner et al., 1953), it presented a significant obstacle to the acceptance of Dart's *Australopithecus africanus* in the general scientific community (Tobias, 1985a:137). The Taung child exhibited features which were exactly the opposite of the preconceived notions of the time. It showed a dentition very similar to that of modern humans, while possessing a brain not much larger than that of a chimpanzee. That an ancestor of our own species had been so chimp-like, so recently, conflicted with the dogma of the age, and it was generally rejected for many long years. This rejection was due partly, though not entirely, to the existence of Piltdown.

Piled on top of the Piltdown forgery was the discovery in the early 1930's of the Peking fossils in China (now attributed to *Homo erectus*). Suddenly the exotic Orient became the center of attention for the study of early human evolution, and again Africa was snubbed in favor of a more agreeable locale. Dart's first visit to England with his new find in 1931 was entirely eclipsed by the announcements of new finds of *Pithecanthropus* (*Homo*) *erectus* (Johanson and Shreeve, 1989:58). Few were convinced of Dart's claims, with some notable exceptions which will be discussed in detail below. It is from these inauspicious beginnings that the study of the genus *Australopithecus* arose.

In time, and with subsequent discoveries, Dart's assertions have been proven to be, for the most part, correct. One of Dart's most ardent supporters was a fiery Scottish geologist named Robert Broom. Broom took it upon himself to augment the known fossil record as much as he possibly could in South Africa. He opened numerous new sites, and for almost every fossil found, proposed a new name, a new species. It is with this legacy of overclassification that this thesis will struggle. We can trace certain trends in the literature of human paleontology which relate to new fossil finds and the proliferation of taxonomic nominae. Broom was one of the most exuberant and productive namers to grace the field of paleoanthropology, and it was he who began the first trend of overclassification within the australopithecines.

It would appear that when there are new hominid sites producing large numbers of new fossils, a splitting trend arises. New fossil discoveries often result in new species being named, and sometimes new genera as well. The exact cause of this overclassification is not certainly established, but some guesses can be made. Certainly the prestige of naming a new species is significant, and claims have been made that this is the reason for all the splitting that goes on. Though this may be a factor, I do not believe it to be the primary one.

As indicated in the introduction of this thesis, one of the key reasons that fossil names accumulate almost as fast as fossil specimens is that researchers are basing their names on different and often incorrect notions of exactly what constitutes a species. Exemplary of this is the work of Robert Broom. Broom apparently utilized what to him was a proper notion of species, the geological species. Different types of rocks, or fossils for that matter, were named accordingly, based on any and all differences, no matter how minor. Geologically this is a sound methodology, though not so biologically. It is in the distinction between geological and biological species that error crept into Broom's interpretations of the hominid fossil record.

As more and more fossils were found, the trend in naming began to abate. Fossils that were once thought to belong to different species became joined in one single species because intermediate forms were found between different fossil morphs. The amount of variation recognized within species was increased as it became apparent in new fossil discoveries. It was eventually recognized that fossils did not have to be identical to belong to the same species. With the light of sober reasoning, a trend developed that saw the number of hominid species being drastically reduced. Researchers began to pay more attention to the similarities between groups, rather than minor differences. Certain species and genera were sunk within previously existing ones, and a more coherent picture of hominid evolution began to emerge.

From the time of the naming of *Australopithecus africanus* until approximately 1953, the trend in species naming continued. It was in 1953 that the Piltdwon forgery was exposed. Subsequent to this, and with the light of sober reasoning, more attention was being paid to the defining characteristics of the hominid species, as well as similarities between the species (not just differences). The exposure and rejection of *Eoanthropus* allowed those researchers who had previously been convinced of its legitimacy to take a closer look at the fossil finds of South Africa. At this point as well, the next generation of paleoanthropologists was being trained, and they brought with them new insights and energy, and left behind the preconceived notions of human evolution of the early 19th century.

The year 1953 not only brought with it the demise of *Eoanthropus*, but *Telanthropus* and *Meganthropus* as well, at the hands of a young South African paleoanthropoloist, John T. Robinson. Robinson brought with him new ideas on human evolution that would change the field entirely, and bring about the transition from almost random species naming (sites equalling species) to detailed consideration of each and every new fossil. The following year, 1954, brought about the demise of *Plesianthropus*, and set the stage for

Robinson's new view about human paleontology. It is therefore in 1953, with the exposure of Piltdown, and the taxonomic reworking of Robinson, that we see a shift in research design and implementation in the field of human paleontology. From this point forward, new species names would be very critically examined, and until 1978, not a single new species name would gain acceptance in human paleontology. A strong lumping trend prevailed, which would allow for the closer analysis of other aspects of human paleontology such as biomechanics, ecology, more detailed anatomy, etc. After the 1953 exposure of the hoax, more attention was paid to the important characteristics *within* the hominidae, as opposed to a continued battle to contrast them with the other great apes.

Subsequent to 1953, new species names were still being generated - albeit at a slower pace - but most were met with skepticism and never accepted. In a seminal work in 1965, Phillip Tobias formally outlined the currently existing hominid species as he saw them, variously sinking those nomina he saw as invalid. Further, he gave firm morphological diagnoses of each species. New fossil finds were now compared to the much enhanced measuring stick that was the enlarged fossil record. The accepted species were *Australopithecus africanus*, *A. robustus*, and *A. boisei*. These remained the only accepted species until *A. afarensis* was named in 1978. Therefore, from 1953 until 1978, a lumping trend prevailed. This trend coincided with a general reduction in the number of new fossil hominids being discovered throughout Africa.

Discoveries of large numbers of fossils in East Africa, as well as the naming of *A. afarensis*, has heralded a new trend of splitting which continues to this day. It thus appears that as new and large quantities of fossils are recovered, new species are named. It is the contention of this study that this trend in naming of new species is a direct result of the recent spate of new hominid fossil discoveries being made over the last 20 or so years in East Africa. This trend follows the earlier one in South Africa in the 1930's and 1940's and in fact mirrors it in many ways. It is also the contention of this study that this trend will also abate, and that with the light of sober reasoning the recent proliferation of new species will end, and that many will be referred to other previously existing species.

To this end, this study will look at the actual diagnostic criteria used to define new species, and will analyze each characteristic with an eye toward determining the actual taxonomic validity of said characteristics. Each accepted species will be delineated, based only on those traits which are capable of separating out extant primate species. It is believed that many if not all of the species named since (and including) *A. afarensis* in 1978 will be found to be lacking.

In order to accomplish this, I will begin by documenting the trends outlined above. I will begin with the early splitting trend of 1925-1953. This will be followed by the later lumping trend of 1953-1978. Finally, I will look at the current resurgence in splitting, from 1978-present. As complete an overview of published paleoanthropological literature as possible will be compiled, along with discussion of the contents of articles and stances of authors. The positions (re lumping and splitting) of the researchers and the effects of their work will be assessed, as will the effects that certain new fossils have on our understanding of hominid evolution, and the ruling orthodoxy of the day.

It should be noted at this point that the term "australopithecine" will be used quite regularily throughout this work. The reason being that most of the different genera and species to be discussed below are now subsumed within the genus *Australopithecus*. By employing the term australopithecine (with a lower case 'a'), I intend to sweepingly refer to all the different taxa which variably include *Australopithecus*, *Plesianthropus*, and *Paranthropus* in one single category for ease of discussion. Australopithecine is a derivation of the term Australopithecinae, which indicated the existence of a distinct sub-family, separate from Hominidae. Whether or not one still accepts the use of the sub-family Australopithecinae, the term 'australopithecine' itself is a commonly used reference which encompasses all fossil hominids that are now held within the genus *Australopithecus* (and for some *Paranthropus*), and will be used as such in this study.

2.2 The Early Period 1925-1953 - The Splitting Trend

Prior to 1925, discussions about potential hominid ancestors revolved more around their presumed closest living relatives than their actual morphological condition. Arguments generally concentrated on exactly which primate could be used as the likeliest ancestor, be it chimpanzees, gorillas, tarsiers, etc. (Miller, 1923). In the absence of any firm genetical data such as we have available today (e.g., DNA hybridization, gene sequencing, electrophoresis, etc.) the true relationships of the primates were unknown, and virtually all different types of primates have at one time or another been proposed as possible ancestors. It was thought though, that the closest living relative was the chimpanzee, and that humans shared a last common ancestor with the chimps and gorillas just prior to their separation from each other (Miller, 1923:244). However, the form of the hypothesized human ancestor was open to so much speculation, and no certainty could ever be held.

It was into this atmosphere of uncertainty, as well as the prevailing dogma regarding early brain expansion as the pivotal event in human evolution, that Dart introduced his species *Australopithecus africanus* (Dart, 1925a). Although he placed the specimen in the direct lineage between humans and apes, he nonetheless felt that the Taung skull was closer to apes than to humans, as can be seen in his naming it the 'southern ape' of Africa. Still, it was an intermediate between living anthropoids and modern humans (Dart, 1925a:195).

Dart listed a suite of characters that separated the skull from known apes, and joined it more closely to humans, but he was particularily interested in the aspects of cerebral development such as the overall skull size, the relationship of cerebral length to facial length, and the development of the brain as witnessed on the accompanying cranial endocast. He attributed increased intelligence for this creature over extant great apes, citing increased cerebral to cerebellar matter than that possessed by gorillas. Based on the forward positioning of the foramen magnum, he also advocated a much more erect stance for these animals than the apes. He felt he had vindicated the claim of Darwin that Africa would be found to be the cradle of humankind.

The reactions to Dart's new find were immediate, and for the most part, negative. The very next week replies had been published in *Nature* by some of the leading anatomists and anthropologists in the world. Sir Arthur Keith indicated that he did not accept the position of *Australopithecus africanus* in the human lineage, stating, "It may be that *Australopithecus* does turn out to be 'intermediate between living anthropoids and man,' but on the evidence now produced, one is inclined to place *Australopithecus* in the same group or sub-family as the chimpanzee and gorilla. It is an allied genus (Keith, 1925a:234)."

Grafton Elliot Smith indicated that he required further evidence to accept Dart's claim, but at the time felt that, "it would be rash to push the claim in support of the South African anthropoid's nearer kinship with man (Smith, 1925:235)." He further stated that the size of the brain placed Taung on the same plane as chimps and gorillas. Sir Arthur Smith Woodward also agreed that the skull appeared to be more closely allied with chimps and gorillas than humans. He also strongly lamented Dart's choice to amalgamate Latin and Greek words to produce the name *Australopithecus*.

The fourth and final comment made on Dart's find came from W. H. L. Duckworth. He appeared much more receptive to the idea of *Australopithecus* being a hominid ancestor, though he was by no means convinced. It is interesting to note that all the replies with the exception of Duckworth's were made by individuals very much involved in the analysis of the Piltdown remains. It is even more interesting to note that the only one of these four commentators to actually mention Piltdown was Duckworth (1925:236). It is quite likely that the vested interests these men had in Piltdown may have colored their views in this matter. They had their preconceived notions about human evolution, and these may quite well have prevented them from objectively reviewing Dart's material. The impossibility of fitting such a small brained ancestor into their desired large brained lineage certainly seems to have slanted their opinions.

Whereas Sir Arthur Keith's first response was somewhat cordial, his next discussion of the Taung skull was much more biting. In mid-1925, Dart allowed a plaster cast of the Taung skull to be displayed in Wembley Hall in London. Keith apparently became quite annoyed that he was not granted special access to the cast, and in fact had to mingle with the common folk to get a view of it (Johanson and Shreeve, 1989:56). In an article in *Nature* in July, 1925, Keith stated:

> An examination of the casts exhibited at Wembley will satisfy zoologists that this claim is preposterous. The skull is that of a young anthropoid ape - one which was in the fourth year of growth - a child - and showing so many points of affinity with the two living African anthropoids - the gorilla and the chimpanzee - that there cannot be a moment's hesitation in placing the fossil form in this living group. At the most it represents a genus in the Gorilla-chimpanzee group.

Incidentally, in the above mentioned single page article, Keith made reference no less than five times to being forced to view the remains in the show case at Wembley. He was by no means convinced of the Taung skull's place in human evolution, and stated that only Java man (*Pithecanthropus*, now *Homo erectus*) was the only known link between man and ape (very strangely making no mention at all of *Eoanthropus* in this respect, in spite of its very simian jaw, that of an orang-utan; Dart had made prominent mention of the chimp-like appearance of Piltdown in his original article).

In a reply to Keith's criticisms, Dart (rather scathingly) indicated that the traits he outlined, in fact, were very different from anthropoid apes, and that it is "not the quantity so much as the quality of the brain that is significant" (Dart, 1925b:462). He felt that Taung skull was significantly different from apes in such crucial ways that Keith's criticisms were unfounded. He further likened Keith's refusal to accept *Australopithecus* to Huxley's refusal to accept *Pithecanthropus* when it was first proposed. Dart's confidence in his appraisal of the Taung skull was both complete and admirable. Keith replied (1925c) that he still believed Dart's claim to be "preposterous", and that the geological age presumed for Taung made it far too recent to be an ancestor to anything other than some form of chimpanzee or gorilla. By this point the discussion between the two had become rather "heated."

Robert Broom had immediately acknowledged the Taung skull as a human ancestor, and although he was almost 70 years old in 1925, he determined to become a great anthropologist (he already considered himself to be the best paleontologist who had ever lived

(Johanson ans Shreeve, 1989:64) - he had published a great deal of extremely important work regarding the transition of reptiles into mammals). Still, it would not be until 1936, when Broom was already 80 years old, that he would make his greatest contributions to human paleontology. However, in 1925, he felt that Taung was a true "missing link" in spite of his assertions that the age of the cave it was found in was rather recent. In an accompanying phylogenetic tree, he placed *Australopithecus* in a lineage extending through *Eoanthropus* all the way to *Homo*.

As a tribute to Broom's brilliance as a comparative anatomist, mention must be made of his discussion of Piltdown. He indicated how remarkably similar *Australopithecus* teeth were to Orang-utan teeth, and then further made mention of the great similarity between *Australopithecus* and *Eoanthropus* (Piltdown was shown to later have had an Orang-utan mandible), thus noting the Orang-utan connection (though not explicitly). He further claimed that, "*Eoanthropus* has a human brain with still the chimpanzee jaw (Broom, 1925:571)." Although Broom did not know that Piltdown was a fake, he recognized from the beginning the association between it and the primates from which it was fabricated.

The first foreign scientist to visit the site of Taung and view firsthand the new skull was Ales Hrdlicka, founder of the American Association of Physical Anthropologists. Although he was quite impressed with the skull, he nonetheless considered it to be no more than a "new species, if not genus, of great apes (Hrdlicka, 1925:392)." He clearly felt that its relationship to the apes was much stronger than to humans, and that it was certainly not a "missing link". As to the age of the site, he felt that the answer could only be achieved after the many fossil baboons from the same site had been adequately studied and compared to other known fossil varieties.

By June of 1925, more detailed analyses had been performed. W. J. Sollas compared the lateral profile of the Taung skull with those of chimpanzees and was able to exclaim that "It is abundantly clear that in a number of significant morphological characters, such as complete absence of the frontal torus, position of the nasion, greater magnitude of the parietal arc, reduced prognathism and shortening of the maxillary region, *Australopithecus* makes a nearer approach to the Hominidae than any existing anthropoid ape (Sollas, 1925:909)." It would appear from this statement that he was willing to accept Taung as a possible human ancestor. This study was later expanded, and Sollas again claimed a position in the human lineage for *Australopithecus,* stating that, "the Taung skull was that of an ape more like man than any other ape yet known (Sollas, 1926:10)."

The following year Dart published a more comprehensive report on the significance of the Taung child. He gave a much more detailed description of the site of Taung, and of the geology and dating of the area. He also discussed what he felt was the ecological adaptation of *Australopithecus*, namely that of a chimp-like animal that relied on hunting and manual manipulation of its environment, and that could survive, by virtue of its enhanced brain, in the harsh environment that was proposed for the time in which it lived (Dart, 1926:321). Again, mid-sagittal sections of the Taung skull, an orang-utan skull, as well as a chimpanzee and gorilla skull, were compared, and it was determined by Dart that although the Taung skull was closest to the chimpanzee condition, there were enough differences of a significant value to separate *Australopithecus* into a different genus and probably a separate family intermediate between the chimpanzee and what was at the time known as *Pithecanthropus* (now *Homo*) *erectus* (Dart, 1926:327).

By 1930 (and in fact today), the question of the geological age of the Taung deposit had not yet been satisfactorily answered. Originally it was thought by Dart's critics that the cave the skull had been discovered in was of rather recent age, and that therefore the skull was too young to be a human ancestor. In 1925 E. L. Shwarz had claimed that the Taung skull was that of a recent primate that had been caught and eaten by "Rhodesian man". In 1930, Robert Broom indicated that he strongly felt the deposits to be Pliocene (Broom, 1930:814), thereby revising his earlier date. It was around this time, the early 1930's, that Broom became very active in the search for South African hominid fossils, and Dart's leading champion in the cause of *Australopithecus africanus*. He would soon discover a number of new and exciting sites which would serve to further bolster the claim of *Australopithecus africanus* against *Eoanthropus* from Piltdown, which had failed to account for any new fossils since the time of Charles Dawson's death in 1916.

Sir Arthur Keith's 1931 book, *New Discoveries Relating to the Antiquity of Man* took Dart's Taung skull to task, devoting the first six chapters of the book to a discussion of the fossil. Keith began by claiming that the Taung cave was far too recent to yield a human ancestor, and that "indeed it is possible, if not probable, that when the Taung skull became embedded in a cave at Buxton, fully evolved man was already an inhabitant of the Harts Valley (Keith, 1931:45)." Morphologically as well, Keith felt that "in all its essential features *Australopithecus* is an anthropoid ape". . . and that "the features wherein *Australopithecus* departs from living African anthropoids and makes an approach towards man cannot be permitted to outweigh the predominance of its anthropoid affinities (Keith, 1931:53)." Regarding the size of the brain, Keith felt that ". . . in the matter of brain endowment *Australopithecus* stands far above the chimpanzee; it was the equal, if not the superior of the gorilla, but falls far short of any standard which can be regarded as human or even prehuman (Keith, 1931:67)." Keith was still of the opinion that brain enlargement was the hallmark of human evolution, and that *Eoanthropus*, *Pithecanthropus*, and *Sinanthropus* were what should be expected in a human ancestor.

Keith next proceeded to compare the Taung skull to skulls of chimpanzees and gorillas and reached the conclusion that "our comparison of skull profiles has led us to a definite conclusion, viz. that the affinities of *Australopithecus* are to be sought for amongst anthropoid apes, not among known human or humanoid forms (Keith, 1931:98)." He came to this conclusion in spite of his acknowledgement that there were no supra-orbital ridges at all on the Taung skull, that in many of the cranial measures he made the Taung skull was well beyond the comparative chimpanzee measures, and that the pterionic region in *Australopithecus* was essentially human in nature. This final point caused him to admit that "in the arrangement of bones in the region of the pterion the Taung skulls reveals a human feature and gives support to Dart's contention that

Australopithecus should have a place in man's ancestry (Keith, 1931:93)." When compared to a gorilla, Keith again made notice of the lack of supra-orbital ridges, as well as the receding nasal region of *Australopithecus*, and the diminutive size of the mandible (compared to the gorilla). In spite of these important differences, he again claimed the anthropoid status of *Australopithecus*.

When discussing the palate and dentition of the Taung skull, it was noted that "in size the palate of *Australopithecus* makes a nearer approach to the human condition than does that of either the chimpanzee or the gorilla. In ratio of palatal area to cranial capacity it is also more human (Keith, 1931:105)." Also, "in its bicanine width and in the development of its milk canines *Australopithecus* is more human than either the chimpanzee or the gorilla (Keith, 1931:106)." It was only in the length of the palate that *Australopithecus* fell into the anthropoid region. Also, estimates of the size of the permanent dentition of the Taung type-skull indicated that the teeth were much larger than human, and actually in the gorilla range. Based on the size of the permanent molar of the Taung skull, *Australopithecus* would "proclaim its full anthropoid nature" (Keith, 1931:107). This was proclaimed in spite of the fact that "the cusps of the molar teeth, in shape and arrangement, are more human than those of the chimpanzee or gorilla (Keith, 1931:107)."

To counter Dart's claims of bipedalism for the Taung skull, Keith discussed the position of the foramen magnum in a juvenile chimpanzee of the same age as the Taung skull. In young chimpanzees the foramen magnum is nearly horizontal on the floor of the skull, and as the animal ages, the foramen is pushed backwards towards the rear of the skull. Dart had compared the position of the foramen magnum with adult human skulls, but Keith claimed that when the comparison was made with a juvenile chimpanzee, ". . . the Taung skull takes its place in the anthropoid, not the human series (Keith, 1931:111)." In conclusion, Keith (1931:115-116) stated that:

> [in] the size and configuration of the brain, the composition of the cranial walls, the features of the face, the characters of jaws and teeth and the manner in which the head was hafted to the neck - leave me in no doubt as to the nature of the animal to which the skull formed part; *Australopithecus* was an anthropoid ape. . . . It was of the same stock as the chimpanzee and gorilla; it is a cousin form. And yet, in other directions it made an approach to the human state - particularily in volume of the brain, in size of milk canines and in the undue persistence of infantile traits. It was certainly more human in its characterization than either gorilla or chimpanzee. . . . In brief the discovery at Taung has given us not a human ancestor but an extinct cousin of the gorilla and chimpanzee.

The only way Keith would have accepted *Australopithecus* as a valid ancestor would be if it had been given a firm dating in the Miocene (though no reason was given as to why the Miocene was so important). Since it was assumed that modern humans had been contemporaneous with the Taung animal, it was rejected as a potential human ancestor.

Early attempts were made to apply biological principles to the analysis of the Taung skull. Paul Alsberg was a strong supporter of Dart and *Australopithecus*, and a powerful voice against the claims of Sir Arthur Keith. Alsberg claimed that "it [the Taung skull] must have [been] much nearer to human conditions than are the anthropoids known so far (1934:157)." He cited as evidence the dolicochephaly of the skull, not seen in any other ape, as well as the extreme reduction in canines of *Australopithecus* compared to gorillas or even chimpanzees. He then looked at the behavior of apes as a functional correlate to their morphology. Gorillas, with their massive canines and large size, were "fighting apes", fully capable of defending themselves against any predator. Other monkeys were fleeing animals, able to hide in the protection of the trees. Because *Australopithecus* was bipedal it could not use the trees, and because it had such small canines, it could not fight in defense. Therefore, Alsberg concluded that it must have relied on its enlarged brain to make tools etc. for defense. Although his biological/cultural interpretations were somewhat weak (as well as colored by overtones of racial strength, a product of his time and place), Alsberg nonetheless asserted that the complex of massive cheek teeth, reduced canines, large brain, and erect posture "points plainly in the human direction (Alsberg, 1934:158)."

The first of Broom's major finds occurred in 1936, at the site of Sterkfontein. Based on a fragmentary skull found there, Broom created the species *Australopithecus transvaalensis* (Broom, 1936a:486). This was an adult version of what, at the time, Broom felt was a similar creature to Dart's Taung baby, though he maintained a specific distinction. After further finds were made, he was able to state that "the premolars and 1st molars are so remarkably human-like that there is scarcely a doubt that had they been found without the skull they would have been held by most to be human (Broom, 1936b:719)." The discovery of an isolated 3rd lower molar later in 1937 further reinforced his view that *Australopithecus* belonged in the lineage leading directly to modern humans (Broom, 1937a:681).

Not everyone accepted this view, and in fact Ernst Schwarz claimed that "these teeth are not human at all but are more like those of the gorilla (Schwarz, 1936:969)." He listed a number of other traits he felt allied the Taung skull with gorillas, and concluded that the Taung skull and Broom's Sterkfontein finds were actually a form of pygmy gorilla, similar to the pygmy status of *Pan paniscus* (Schwarz, 1936:969). Broom replied to this by stating that "Dr. [William King] Gregory. . . has pointed out that of twenty-six dental characters in *Australopithecus*, not one is nearer to the chimpanzee, two are nearer to the gorilla, one is nearer to the chimpanzee and the gorilla, three are common to the chimpanzee, gorilla, and primitive man, and twenty are transitional to or nearer to primitive man (Broom, 1937b:326)." Further fossil finds strengthened Broom's conviction that the teeth were not at all similar to apes, but were almost human in form; he stated "one might describe *Australopithecus* as a chimpanzee with human teeth (Broom, 1938a:829)."

Broom's opinion regarding his species *Australopithecus transvaalensis* changed slightly in 1938, when he indicated that he then felt that the Sterkfontein finds were different enough from Taung to require the creation of a new genus, *Plesianthropus* (Broom, 1938b:377). This generic distinction was based on rather scanty evidence, namely that "the shape of the [mandibular] symphysis is so different from that of the Taung ape that it seems advisable to place *Australopithecus transvaalensis* in a distinct genus, for which the name *Plesianthropus* is proposed (Broom, 1938b:377)."

In the same article, Broom further named another new hominid genus and species, *Paranthropus robustus*. This species was based on a fragmentary skull found at the site of Kromdraai, a mere stones throw from Sterkfontein. About this new find Broom claimed "the 2nd premolar differs very markedly from that of *Plesianthropus transvaalensis*, and we may thus confidently place the new skull in a new genus and species (Broom, 1938b:378)."

Again, a new genus was erected based on some extremely flimsy evidence. There was some further discussion by Broom about some other dental differences (1938b:378), but this genus was still named perhaps prematurely. This is an especially important point as regards this thesis. There is a current resurgence in the use of the generic nomen *Paranthropus*, with certain researchers (Clarke, 1976, 1985; Grine, 1981, 1985, 1988a,b; Olson, 1981, 1985; Robinson, 1962, 1963, 1972a,b; Susman and Brain, 1988; Susman, 1988; Wood and Chamberlain, 1987) claiming that the genus was and is distinctive enough to warrant such a separation. This discussion will receive a much more in-depth treatment later in this study, so suffice to say at the moment that the tenuous nature of this genus was present from its initial naming.

In 1938 some post-cranial fragments of early hominids were found both in Kromdraai and Sterkfontein. Broom indicated that the morphology of the post-cranial elements was so similar to modern human that they were almost impossible to distinguish (Broom, 1938c:897). This was further evidence of the similarity of *Australopithecus* to humans, and the direct lineal descent. The editors of *Nature* magazine appeared inclined to agree with Broom on this point. They stated that his evidence fully bore out the conclusion that *Australopithecus* was "nearly human". The bipedality of *Paranthropus* and *Plesianthropus* convinced them that they were in fact discussing human ancestors.

Other researchers were also being convinced of the reality of Dart's conclusions. William King Gregory, one of the foremost paleontologists at the American Museum of Natural History was a strong supporter of *Australopithecus* as an ancestor in the human lineage. Along with Milo Hellman, he visited South Africa in 1938 to get a closer look at the fossils, and came to the conclusion that the various genera and species of the australopithecines were in fact intermediate between humans and chimpanzees (Gregory and Hellman, 1938:614).

Although Gregory had apparently accepted the existence of *Eoanthropus dawsoni*, he had also, in fact, insinuated as early as 1914 that the fossils might be fake. He had visited London in the summer of 1913, and had apparently been privy to some discussions regarding the Piltdown forgery. He wrote "It has been suspected by some that geologically [the Piltdown fossils] are not old at all; that they may even represent a deliberate hoax, a negro or Australian skull and a broken ape jaw, artificially fossilized and "planted" in the gravel bed to fool the scientists (Gregory, 1914:190)." In the article he also published plates of orang-utan jaws which show the near identical match between the them and the Piltdown mandible. There were others who also refused to accept Piltdown as a valid ancestor. In 1915, Gerrit S. Miller claimed that the mandible was that of a chimpanzee which he named *Pan vetus*. Weidenreich considered the

Piltdown mandible to belong to an orang-utan-like ape. Friederichs went a step further and named a new orang genus and species for the mandible, *Boreopithecus dawsoni*. In spite of this dissention, and in spite of the fact that Gregory had been lead to his statement by someone knowledgable in London, the warnings were ignored, and *Eoanthropus* held sway for almost 40 more years before being exposed. Piltdown too well fit the idea of the time of what was the "proper" ancestor for humans to have.

The status of *Australopithecus* as an intermediary between humans and apes was further enhanced as Gregory and Hellman expanded on their earlier detailed analysis of the South African fossils. They were to eventually claim that the australopithecines evolved out of the *Dryopithecus-Sivapithecus* stock and into the human stock, presumably passing through a *Sinanthropus-Pithecanthropus* (now *Homo erectus*) phase (Gregory and Hellman, 1939:564). Detailed comparisons of the teeth of *Proconsul*, *Sivapithecus*, *Sinanthropus*, *Gorilla*, *Pan*, and *Homo* all pointed toward a phyletic relationship between the australopithecines and modern humans. It was claimed that the modern human dentition evolved out of an australopithecine one (Gregory and Hellman, 1939:564).

At this point, it can be noted that the distinction between *Sinanthropus* and *Pithecanthropus* was being strongly questioned. Soon after *Sinanthropus* was named, Solly Zuckerman claimed that it was merely a new species of the already named *Pithecanthropus* (Zuckerman, 1931). The eminent Oxford anatomist, Wilfrid E. Le Gros Clark stated, in a 1937 article in which he was replying to a claim by Professor Eugene Dubois, that "*Pithecanthropus* was not a man but a gigantic gibbon" that, in fact, "the similarity of the *Pithecanthropus* calvarium and endocranial cast to those of *Sinanthropus* is so close that they can be argued with some reason to be the reamins of a common genus of primitive man (Le Gros Clark, 1937:62)." He furthered this argument in 1940 by proposing that the genus name *Sinanthropus* be formally sunk in favor of *Pithecanthropus* (Le Gros Clark, 1940:70). He actually favored not even a specific distinction between the two groups of fossils, an argument that agreed with Weidenreichs' assessment of the Peking fossils as being only racial variants of the species *Pithecanthropus erectus*. Foreshadowing this present study, Clark further indicated that we should carefully examine "the whole question of the validity of the morphological evidence upon which physical anthropologists often seem to depend for their taxonomic conclusions (Le Gros Clark, 1940:70)." On the point of the lack of distinction between *Sinanthropus* and *Pithecanthropus*, Clark was in agreement with others such as Zuckerman and as von Koenigswald and Weidenreich.

In 1940, Dart provided a brief summary of the controversy that had surrounded the Taung skull since its discovery 15 years earlier. He described and commented on the ape-like characteristics it had, the uncertain dating of the site itself as well as the skull, and the supposed lifestyle these early hominids displayed. He further listed numerous morphological traits which evidently separated the australopithecines from the living apes. Regarding the endocranial cast that accompanied the Taung skull, Dart gave a detailed discussion of the exact features he saw as making the brain of this animal sufficiently superior to the ape brain as to place it in the human lineage (Dart, 1940:180). For Dart, *Australopithecus* was an ape-man well on the way to human status, and "there is no known anatomical feature of *Plesianthropus* or *Paranthropus* which is not human unless it be the endocranial volume (Dart, 1940:184)." Since he felt, along with Sollas and with Alsberg, that the actual brain volume was of little significance, he stated that the australopithecines "should be assembled with the Hominidae as the most primitive types of man hitherto discovered (Dart, 1940:184)."

The drastic taxonomic splitting of the time was also not limited only to the australopithecines. Within the genus *Homo* there was also a rapid profusion of new names. They were essentially names for each new fossil found, and little by way of comparison was done between them (rather, every minute detail that separated different fossils was closely studied). Species names like *Pithecanthropus erectus* and *Pithecanthropus pekinensis* were used freely, even after the genus *Sinanthropus* was sunk in favor of *Pithecanthropus* (creating *P. pekinensis*) by Weidenreich. *Palaeoanthropus heidelbergensis*, *P. ehringsdorfensis*, *P. neanderthalensis*, *P. krapinensis*, *P. palestinensis*, *P. rhodesiensis* were all named for Neanderthal skeletons (Gates, 1944:282). Most species names were erected for single fossil finds, and all today are subsumed within *Homo sapiens* (although there is a current resurgence of the name *Homo neandethalensis* for all Neanderthal material). *Homo australicus*, *H. capensis*, *H. africanus*, *H. mongoloideus*, and *H. caucasicus* represented five different species of modern or extinct humans; essentially the main racial varieties were elevated to the level of species (Gates, 1944:288). This is the most blatant example of the lack of application of any biological principles to the naming of species, and it also underlines the racial overtones current in anthropological thinking at the time. All this splitting was done in spite of the work of such men as Weidenreich, Le Gros Clark, and Mayr which showed that a significant amount of overclassification had gone on.

The insufficiency of the traits used in the past to name new species and genera of hominids can again be seen in the work of Robert Broom. When a mandible of an immature fossil hominid was discovered at Kromdraai, Broom compared it to the known mandible of the Taung child. He claimed that "when the teeth are compared with those of the Taung ape (*Australopithecus*) it is manifest that the two young forms belong to different genera (Broom, 1941a:607)." As evidence, he published drawings of the Taung mandible, the new mandible, as well as mandibles from a human, a baboon, and a chimpanzee. Different genera were proposed for the fossils because *Paranthropus* had a smaller incisor and canine than *Australopithecus*, a different cuspal arrangement and shape of the first deciduous molar, as well as a different size and cuspal arrangement of the second deciduous molar. Broom claimed that the two genera ". . . cannot be closely allied" when compared to each other, but that when compared to humans "there must be some close affinity (Broom, 1941a:607)." Later, more deciduous teeth were found, leading Broom to claim that "the presence of a distinct Carabelli cusp on the 2nd milk premolar of *Plesianthropus* seems to show that this ape-man is very nearly related to man, and not closely related to the living apes (Broom, 1947a:602)."

One of the main reasons for Broom's tendency towards overclassification may stem from his reliance, perhaps overreliance, on the geological ages ascribed to the fossil sites. He stated as a prime reason for placing *Paranthropus* fossils in a distinct genus from *Plesianthropus* the fact that they were derived from different geological ages (Broom, 1941b:12). In the same paper, Broom also made the curious statement that he felt it quite improbable that any of the South African hominids were actually ancestral to humans. He believed that they were in fact closer to gorillas than to chimpanzees, though he gave no concrete reasoning why he believed this to be. In his accompanying phylogenetic tree, he indicated that the australopithecines branched off from the main hominid line in the late Pliocene, and subsequently went extinct, without issue.

Broom was the first to publish a comprehensive analysis of the australopithecines in 1946 in a monograph put out by the Transvaal museum in Pretoria. In this volume, he discussed the fossils, anatomy and taxonomy of the three named genera of the time, *Australopithecus*, *Plesianthropus*, and *Paranthropus*. To begin with, Broom described some of the controversy that first surrounded *Australopithecus*, as well as the opinions of some prominent researchers. He then moved on to a discussion of some of the associated fauna found at Taung (it must be remembered that at that time, sites still equalled species i.e. Taung = *Australopithecus*, Sterkfontein = *Plesianthropus*, and Kromdraai = *Paranthropus*, and there was no overlap of species and sites). Broom quite forcefully accepted Dart's earlier view that these associated faunal remains were the result of the predatory habits of the australopithecines, citing the fractured skulls of baboons as evidence of hunting with stones or sticks (Broom, 1946:28).

Broom proceeded next to give a very detailed analysis of the morphology of the Taung skull (then the only know specimen of *Australopithecus africanus*). A common theme in these early discussions was the distinction of *Australopithecus* from the great apes, especially the chimpanzee and the gorilla. Until the official debunking of Piltdown in 1953, the prime consideration was to show these fossils to be human ancestors, closer to *Homo* than to any ape. This makes for difficult testing of these traits, as the distinctions are those which separate the australopithecines from my chosen outgroup. Nonetheless, morphological characteristics separating the various australopithecine species and genera were made, and it is these which are used for this study.

For both *Plesianthropus transvaalensis* and *Paranthropus robustus* Broom again gave very detailed descriptions of all the known fossils, as well as any associated fauna recovered from the sites. He further listed numerous anatomical traits that he felt separated the various genera from each other, particularily *Plesianthropus* from *Paranthropus*. These included the characteristic flattening of the face (the dished face of the australopithecines), the point of origin of the zygomatic process, anterior buttressing, brain size, foramen magnum position, as well as a large quantity of dental traits. It is these morphological characteristics which will be analyzed by the current study.

Unfortunately, Broom's discussion of *Australopithecus* is somewhat lacking in this volume. He apparently preferred to rest his argument for this generic distinction on past works, as there was only the one specimen of *Australopithecus* at the time, and it had been thoroughly studied by previous authors. He made a number of statements regarding *Australopithecus*, however, that do deserve mention. From these we can again see the level of overreliance on small numbers of morphological characteristics in the naming of new genera and species.

Broom recognized the difficulty in separating the different australopithecine genera from the Taung ape; "whether the Sterkfontein ape, which there is good reason to believe is generically distinct from that of Kromdraai ape, is also generically different from the Taung ape is a little more difficult to settle (Broom and Schepers, 1946:128)." He rested his argument on the deciduous dentition, as this was all that was known at the time of *Australopithecus*. He stated "the milk teeth of *Paranthropus* are so very different from those of *Australopithecus* that there cannot be any doubt that the Kromdraai ape must be placed in a different genus from the Taung ape" and that "the imperfect lower first milk molar of the Sterkfontein ape is so different from the corresponding tooth of *Australopithecus* that it confirms the opinion that the two forms are genrically distinct (Broom and Schepers, 1946:128)." He stated this with full knowledge that "there are those who hold that the Sterkfontein and Kromdraai skulls are merely adult skulls of *Australopithecus*. . . (Broom and Schepers, 1946:128)." Broom was convinced of the distinct generic status he accorded his apes.

In April of 1947, a beautifully preserved, almost complete skull of *Plesianthropus* was discovered at Sterkfontein, and it was dubbed Mrs. Ples in honor of the species to which the presumed female belonged (Broom, 1947b:672). The complete condition of the skull was of great interest, and Broom hoped that "the *Plesianthropus* skull will be almost as satisfactorily known as that of man or any of the living apes (Broom and Robinson, 1947:809)." A brief discussion of two important features of the skull was later given, to show the proximity of the specimen to the human condition. A more complete discussion was saved for a later volume on *Plesianthropus* which will be discussed below. The relations of the sphenoid, ethmoid and frontal bones have a distinct structure in humans which is different from apes. The new skull of *Plesianthropus* showed that in the anterior fossa of the cranial cavity, the sphenoid forms a large part of the floor of the fossa and articulates with the ethmoid, a condition not seen in the great apes (Broom and Robinson, 1947:809). Also, "in man the inner wall of the orbit is mainly formed by the lacrimal, the frontal, the ethmoid and the maxilla . . . [and] the orbital wall in *Plesianthropus* shows a condition almost exactly as in man (Broom and Robinson, 1947:810)." These features again showed Broom as well as his audience "that the Australopithecinae and man are very closely allied, and that these small brained man-like beings were very nearly human (Broom and Robinson, 1947:810)."

The tide began to turn in favor of the hominid status of the australopithecines in the late 1940's, especially after the eminent Oxford anatomist Wilfrid Le Gros Clark added his considerable support to the claims of Dart and Broom. Le Gros Clark felt that ". . . the human resemblances in the skull, dentition, and limb bones [of the australopithecines] are so numerous, detailed and intimate as virtually to preclude the introduction of the idea of 'parallel evolution' in order to explain them. In other words, there must be a real zoological relationship between the Australopithecinae and the Hominidae (Le Gros Clark, 1947:145)." After examining the fossils firsthand in South Africa, Le Gros Clark claimed that ". . . the Australopithecinae represent by far the most important discoveries which have so far been made in the field of human paleontology", and that . . . "the resemblances which they show to man in the morphological features of the skull, dentition, and limb bones are so remarkable that their zoological relationship can hardly be doubted (Le Gros Clark, 1947:173)."

The article in which these strong words appeared was a seminal work on the anatomy of the australopithecines, published in the prestigious *Journal of Anatomy*. Le Gros Clark had pulled together into one work basically all the anatomical information that had been published over the years by Dart, Broom, and others. One of the reasons for the writing of the article was to admit the fact that ". . . in the past, several anatomists of recognized distinction have, by their misinterpretation of the evidence, tended to belittle [the fossils'] importance (Le Gros Clark, 1947:143)." He was clearly attempting to set the record straight as regarded human paleontology, and this involved first accepting the hominid status of the australopithecines, and second, disproving the validity of the *Eoanthropus* fossils. Le Gros Clark was in fact one of the three scientists who eventually exposed the Piltdown hoax (Weiner, Oakley, and Le Gros Clark, 1953).

The firm acceptance by Le Gros Clark of the hominid status of *Australopithecus* set the stage for the general reception of these new ancestors into the human lineage. His study quite likely prompted him to take a much closer look at the Piltdown remains. His subsequent book *The Fossil Evidence for Human Evolution* (1955) completed his analysis, and helped to change the face of human paleontology. After this point in the late 1940's and early 1950's the emphasis shifted from proving the australopithcines were not apes, to delineating their exact taxonomic status, and the proper phylogenetic sequence that gave rise to the genus *Homo*.

It was this slight shift in focus that also served to allow the sober reasoning of other researchers to begin to compare the fossils to each other (rather than to chimps and gorillas), and to begin to lump them together in better approximations of biological species than had been done previously. If one requires an exact time frame when this shift in research focus took place, I would say then that it was with the exposure of the Piltdown fraud that human paleontology changed irrevocably. However, this change began with the sober reasoning of men such as Le Gros Clark in the late 1940's who allowed, in the words of E. A. Hooton "a dispassionate interpretation of new fossil evidence [which] is usually obtainable only when one awaits the reworking of the material by persons not emotionally identified with the specimen (1938:114)." The change that Le Gros Clark helped to preciptate was still a slow one, and the taxonomic overindulgence continued for a number of years yet.

In 1948, the next new hominid fossil species was named by Raymond Dart. A fossilized occipital bone was found in the limeworks of a site known as Makapansgat. Dart recognized it as being from an upright walking individual with hominid characteristics allying it closely to *Australopithecus*. He went to great pains to compare the specimen to known examples of *Sinanthropus*, *Pithecanthropus*, *Plesianthropus*, *Pan* and *Gorilla*. As a result, he was able to show that indeed the new fossil was not that of an ape, but in fact a member of the genus *Australopithecus*. He felt that there were sufficient differences to create a new species, and he thus named *Australopithecus prometheus*. To anyone familiar with Roman mythology, the name 'prometheus' has an added connotation. Dart believed that he had evidence of the earliest use of fire by this new species (Dart, 1948:276). He noted the presence of numerous fractures and splits in the bones of other mammals found on the site, as well as in the bones of the australopithecines. It was from this evidence that he developed his ideas about the carnivorous and cannibalistic habits of the australopithecines.

Eventually *Australopithecus prometheus* would be sunk into *Australopithecus africanus*, a move that was foreshadowed by Dart in his original article. Based on work that Broom had been doing on the mammalian fauna associated with the various hominid bearing sites, Dart questioned whether the differences in fauna found at Makapansgat and at Taung could relate more to climatic differences than to geological or temporal discrepancies, and then added that "In that event we might be confronting at Makapansgat merely the adult form of the large brained *Australopithecus africanus* (Dart, 1948:278)." However, Dart firmly believed that the cultural differences he noted, namely the hunting and fire use of

Australopithecus prometheus, as well as some anatomical differences, mitigated against this argument.

In his discussion of the status of *Plesianthropus*, Dart felt that the generic distinction between it and *Australopithecus* was becoming increasingly untenable, especially in the light of new fossil discoveries and new scientific concepts being applied (although he didn't say so, it is quite likely that Dart was referring to the then new biological species concept of Mayr; his discussion of the behavioral evidence of his new species does appear to take into account certain tenets of this then new concept). He believed it probable that ". . . the whole 'sub-family' of Australopithecinae have nothing more than 'generic' rank within the 'sub-family' Hominidae (Dart, 1948:279)." He also revised his ideas on the proximity of *Australopithecus* and modern humans. Instead of just being 'man-apes', closer to the ape condition than to the human, Dart now felt the australopithecines were ". . . pre-palaeolithic man in his various forms . . . (Dart, 1948:275)." They were now seen to be so close to humans that Dart agreed with the lamentation of Sollas that he had not named his genus *Homunculus* to denote its nearness to humans. Man-apes no more, they were now direct human ancestors.

The following year yet another new hominid fossil species was named, *Paranthropus crassidens*. This new species was named by Robert Broom to encompass the fossil material that was being found at the new site Swartkrans, again, a stones throw from Sterkfontein and Kromdraai. Again, the fossil evidence for this new species is extremely scanty. Broom found a mandible and some isolated teeth, and because they appeared larger than those of *Paranthropus* *robustus*, he created a new species. He also stated that "when a new skull is discovered it may prove to belong to another genus (Broom, 1949:57)."

Clearly the sober reasoning of those not emotionally attached to the fossils was more necessary than ever. Again in this paper we can see the zealous use of taxonomy to distinguish the smallest of differences. Broom made note of the new species *Australopithecus prometheus* of Dart, and "though I am not convinced that he made fire, I am of the opinion that the being belongs not only to a new species, but to a new genus (Broom, 1949:57)." Dart had made his original claim based on an occipital fragment, and upon the presumed use of fire. Broom was ready to create a new genus based on the occipital fragment only, as he was unconvinced by the evidence of fire at the site (Dart's major concern). The taxonomic splitting was reaching monumental proportions.

Later that same year, yet another new genus and species was named by Broom and Robinson, *Telanthropus capensis*. A fossilized mandible had been found at Swartkrans which was ". . . fairly manifestly a new type of man (Broom and Robinson, 1949:322)." Based on a few differences of the mandibular symphysis, ramus, and the three molars, a new genus was erected. The affinities of this new species were ". . . somewhat allied to Heidelberg man", because the jaw itself ". . . in general structure comes nearest to that of Heidelberg man (Broom and Robinson, 1949:322)." They believed the new find to be intermediate between the australopithecines and the genus *Homo*. This species, however, did not have a long life, as one of its namers, John Robinson, subsequently sank it in favor of what he would come to call *Homo transvaalensis*, one of his 'true' hominids.

Fossil finds representing *Australopithecus prometheus* were still being uncovered, and in 1948 a well preserved pelvis was found at Makapansgat. This find allowed the first look at this critical anatomical region, specifically at the erect bipedal form of locomotion proposed by Dart to characterize *Australopithecus*. Dart was able to conclude that "the innominate bone in *Australopithecus prometheus* is utterly unlike that of the semi-erect chimpanzee, but on the contrary resembles closely that of the living *Homo sapiens* (Dart, 1949:301)." This was a crucial bit of evidence in favor of Dart's claim for *Australopithecus* as a human ancestor. Coupled with the knowledge from Makapansgat of the forward position of the foramen magnum, as well as some other limb bones (particularily the distal femur of *Plesianthropus*), Dart's claim at least for bipedalism was becoming airtight.

Based on this find Dart extended his views on the predatory nature of the australopithecines by claiming that "the prime reason for the liberation of man's hands, as Darwin recognized, was their increasing employment in manipulating clubs and missiles. This industrial specialization of the hands in accurate hitting and throwing did not follow but rather provoked the very series of anatomical and physiological changes throughout the body (Dart, 1949: 330)." Dart felt that australopithecines had become bipedal to free the hands "to achieve accuracy in breaking bones, whether with sticks held in hands or with stones flung from hands (Dart, 1949:330)."

The so-called 'killer apes' were born, and the Osteodontokeratic culture of Dart would soon be revealed. "This accuracy in hitting and hurling, which apes lack but men universally possess in such high degree for it to amount to an inherited instinct, does not necessarily connote a highly developed brain; it demands no greater intelligence than is possessed by human microcephalic idiots with australopithecine cranial capacities (Dart, 1949:331)." William King Gregory, while accepting Dart's interpretations of the predatory nature of the australopithecines, indicated that they "were also general feeders or even in part carrion feeders, alert to snatch away from the vultures the remains left by lions and hyaenas (Gregory, 1949:503)." This idea, though not widely held at the time, strongly foreshadowed the now held belief of what some of the food gathering techniques of the australopithecines were (see Blumenschine, 1991, for a more detailed analysis of hominid carnivory and food gathering strategies).

In 1950, Robert Broom produced a summary article entitled *The genera and species of the South African fossil ape-men*. In it he outlined the evidence for the construction of the five types of ape-men that were then recognized in South Africa. Broom was discussing the supposed validity of the various species then ascribed to the genus *Homo*. He began early with the statement that "scientists who are unaquainted with the mode of occurrence of these fossils are naturally inclined to consider that possibly all our ape-men fossils are contemporaneous, and probably all belong to one species (Broom, 1950:1)." It is this statement that Broom apparently wished to contend. He was arguing the point of the splitter versus that of the lumper.

Broom lamented the lack of further fossil finds from the Taung site, and indicated that it would be very difficult to match an adult skull from another site to the juvenile Taung skull. The only recourse available for dating the site (then and now) was through faunal associations, and none of the other sites in South Africa matched exactly the fauna found at Taung. When the *Plesianthropus* material of Sterkfontein first came to light, as Broom mentioned, there was no way to compare it to the Taung baby. They therefore had to rely on the associated fauna of the sites, and since there was no overlap at all between the fauna of the two sites, Broom felt that the two types had lived in significantly different environments, implying different econiches, and they therefore deserved taxonomic distinction. To Broom, the significantly different environmental conditions of such close (only 200 miles distant) sites warranted the naming of different species.

Later discoveries at Sterkfontein brought forward some deciduous teeth, but it was noted that the canine of the Taung baby had apparently only 2 cusps, while *Plesianthropus* had 3. Based on this Broom was able to proclaim that "of course we know how variable the canine may be; but we may feel very certain that such different canines belong at least to different species and there seems considerable probability that they belong to different genera (Broom, 1950:4)." Broom next discussed the deciduous lower first molars. *Paranthropus* had 5 main cusps and a marked anterior fovea. *Australopithecus* possessed 4 cusps, with a reduced anterior fovea pushed to the side. Broom stated that "here the structure of the tooth differs so very markedly that in my opinion *Paranthropus* not only cannot belong to the same genus, but will probably have to be placed in a distinct sub-family (Broom, 1950: 4)." To call Broom a splitter would be an understatement.

Discussing *Paranthropus robustus*, Broom noted that a child's mandible had been found, and because of that mandible ". . . we can be quite sure that *Paranthropus* is a very distinct genus from *Plesianthropus*. And having such conclusive evidence from the milk teeth it is unnecessary to discuss the differences of the adult skulls (Broom, 1950:6)." Apparently enough had been said about that point. Regarding *Australopithecus prometheus*, Broom mentioned that "while I am not satisfied with the evidence that these ape-men made fire, I am fully convinced that they belong to a very distinct species. But I consider that they cannot belong to a species of *Australopithecus* (Broom, 1950:7)." Another new genus was required to encompass some anatomically very similar (if not identical) specimens. In Broom's opinion, ". . . the Makapan ape-man belongs to quite a distinct genus, and probably to a distinct sub-family (Broom, 1950:8)."

For *Paranthropus crassidens*, the difference in size of the teeth was enough to place it within a new species, apart from *Paranthropus robustus*. Based on the find of a juvenile mandible at Swartkrans, Broom was pleased with the match with Kromdraai, and therefore pleased that the two were placed in the same genus, though still requiring separate species (again, based on the overall tooth sizes). Foreshadowing today's greatest controversy in all of paleontology, Broom indicated that "of course as we get more and more connecting links and have the whole chain from *Australopithecus* to man, classification will become more and more difficult. . . . We will be unable to say what is ape-man and what is true man (Broom, 1950:12)."

Broom was apparently giving extreme weight to the faunal associations of the various sites, to the exclusion of solid morphological analyses. He noted that the fauna from each of the sites were different, and then to support these distinctions, he looked for some oft-times minute morphological differences in the hominid fossils. To him, different faunas meant different ages and different environments, and these equated to different taxa. Broom also advocated the liberal use of higher taxa as well, requesting the construction of three sub-families to house the australopithecines: Australopithecinae to house *Australopithecus africanus* and *Plesianthropus transvaalensis*, Paranthropinae to house *Paranthropus robustus* and *Paranthropus crassidens*, and Archanthropinae to house *Australopithecus* (?) *prometheus*. Taxonomic naming was "only a matter of convenience, and I think it will be much more convenient to split the different varieties into different genera and species than to lump them (Broom, 1950:13)." This statement is quite indicative of the improper notion of species held by early taxonomists, particularly Broom.

The second of the major australopithecine monographs was published by the Transvaal Museum in 1950, entitled *Sterkfontein Ape-man Plesianthropus*. Authored by Broom, Robinson and Schepers, this volume took a somewhat different tack than the previous *Australopithecinae* volume. Rather than trying to convince the reader of the human-like qualities of the fossil material, the authors chose instead to give extremely detailed descriptions of the best preserved fossils, and to leave the conclusions to the audience. One of the major reasons behind this decision must have been the fact that, for the most part, *Australopithecus* had been generally accepted as a valid human ancestor, even by its most vocal opponents. Sir Arthur Keith himself, in a private communication to Robert Broom in 1947 said "no doubt the South African anthropoids are much more human than I had originally supposed (Broom, 1951:60)." In fact, in the conclusion of the volume, a long list is given of eminent scientists who had come to accept the australopithecines as being human ancestors (Broom, et al., 1950:76).

Most of the rest of the conclusion was a discussion of the human lineage, specifically, from which primate line humans evolved. It was assumed that humans evolved through the australopithecine stage into modern *Homo*, but from what ancestor did the australopithecines evolve? Broom et al. felt that "all the evidence from the dentition is in our opinion in favor of man having been derived from a pre-anthropoid (Broom et al., 1950:80)." Essentially, based on the morphology of the teeth, it was presumed that humans were not descended from the apes, but rather split off earlier. "It seems to us clear that neither man nor the Australopithecids can be at all closely allied to any of the anthropoids at present alive, or to any of the known fossil ones, except *Propliopithecus*. . . . This early Egyptian form must we think be pretty closely allied to the human and Australopithecid ancestor

(Broom, et al., 1950:82)." These statements were made without the benefit of the genetical data we now have which shows our close relationship to the chimpanzee, but are again indicative of the overreliance placed on certain small differences. In spite of all the similarities between chimpanzee teeth and human teeth, enough minute differences were distinguished to deny apes and humans any close relationship.

Further to Keith's eventual acceptance of *Australopithecus* as being a valid human ancestor, Keith publicly proclaimed "I am now convinced, on the evidence submitted by Dr. Broom, that Prof. Dart was right and that I was wrong (Keith, 1947:377)." Admitting one's error is a truly rare occurrence in science.

Within a year of the taxon *Telanthropus capensis* being erected, it was under attack. Of special significance to this study is the kind of attack that it faced. When Broom and Robinson first named the new species, they claimed that "the mylohyoid groove runs up to the foramen as in typical human skulls. . . . The typically human mylohyoid groove in our supposed man, and the certainly not typically human groove in *Paranthropus*, seem to make it certain that the two jaws belong to different genera (Broom and Robinson, 1949: 323)." William Struass took issue with this point, and indicated that this "so-called 'human' type of mylohyoid groove is highly characteristic of man but also of one great anthropoid ape and at least one Old World monkey (Strauss, 1950: 497)." The important point here is that Strauss was calling for an analysis of *intrageneric variability* of the trait. Because this form of mylohyoid groove was incapable of separating out *Telanthropus* from an ape form (the gorilla), Strauss felt that ". . . the value of the groove-foramen relationship is thus highly limited, and *its phylogenetic significance - if any - obscure* (Strauss, 1950:498 italics mine)."

With the phylogenetic validity of this important trait called into question, the validity of the new species was also called into question. The attack that *Telanthropus* faced mirrors that which the australopithecines face in this study, and the validity of the traits used to name and define the australopithecines will be determined much as it was in 1950. That the species was coming under attack at the time was indicative of the new approach that was being taken to hominid systematics. The species were coming under review, and the superficial differences in morphology used to define the australopithcines were being much more closely analyzed. The lumping trend was about to begin.

A first tentative step in the lumping direction came not from within human paleontology, but from without, in the form of a biological systematist whose own specialty was the taxonomy of birds. Ernst Mayr, now famous for his biological concept of species, the most comprehensive and useful definition of species used today, took a look at the taxonomy of the early hominids and saw a number of problems. Mayr began by criticizing the proliferation of taxa among the fossil hominds, stating "some anthropologists, in fact, imply that they use specific and generic names merely as labels for specimens without giving them any biological meaning (Mayr, 1950:109)." When he looked specifically at the australopithecines, Mayr claimed that ". . . I did not find any morphological characters that would necessitate separating them into several genera (Mayr, 1950:110)." His solution was to sink all of the australopithecine genera in favor of *Homo*, with three species housed within it. Mayr would recognize *Homo sapiens* for modern humans, *Homo erectus* for the Java and Peking finds, and *Homo transvaalensis* to encompass all of the South African fossil material (Mayr, 1950:113).

Mayr believed that "there is nothing in the evidence that has been so far presented that would prove that more than one species is involved (Mayr, 1950:113)," and thus felt justified in sinking all of the South African material into one species. He felt that "to consider [all the South African material] as one species is the simplest solution that is consistent with the available evidence (Mayr, 1950:114)." He was at the time employing Occam's Razor, and it would only be with future discoveries that the distinction between the 'robust' and 'gracile' australopithecines would become more apparent. The human lineage was essentially one single line of descent from the apes, through the australopithecines stage, and into the modern human stage. Since only one lineage was represented, no speciation event had been passed, and therefore only one species was represented in our lineage. Moving beyond the australopithecines, Mayr further contended that chimpanzees and gorillas belonged to the same genus, and that the Hominidae was invalid as a separate family from the pongids. Mayr was a lumper's lumper.

In the discussion following Mayr's paper (presented at the Cold Spring Harbor Symposium on Quantitative Biology), all of the commentators agreed with Mayr that far too much invalid taxonomic splitting had taken place, and that his revision was necessary. However, it was believed by most paleoanthropologists that Mayr had gone too far in his lumping, and that his revised phylogeny would obscure that true nature of the relations between the different species of australopithecines. His claim of no more than one hominid species ever living at one time would soon be demonstrated to be incorrect, and the cerebral distinctions between *Homo* and *Australopithecus* would be accepted by some as warranting the generic distinction.

Nonetheless, the opinion of an external reviewer, a systematist by profession, helped to revolutionize the taxonomy of the australopithecines, and future discussions would be far more biological in nature. Gone, at least for the time being, would be the trend of granting of names to every new fossil found. Instead, species of fossil hominds became biological units that were once living, breathing animals. The relations between these biological units would take over as the prime directive of anthropologists, and a more realistic picture of human evolution would begin to take shape.

In 1951, Robert Broom wrote a rather publicly oriented book called *Finding the Missing Link*. In it he detailed the important discoveries that had been recently made in paleaonthropology, both in South Africa, Europe, and Asia. In it he lamented the poor treatment Dart's discovery had received, and chastized the scientific establishment for failing to recognize the importance of the Taung skull. He did not hold back at all, ridiculing American and British scholars for their lack of foresight. However, when he discussed the taxonomic allegiances of the fossils, Broom claimed that a juvenile mandible found at Sterkfontein "shows that *Plesianthropus*, though allied to *Australopithecus*, is generically distinct, as I had held for over ten years (Broom, 1951:72)." The splitting never subsided. Making notice of the fact that few researchers accepted his generic distinction for *Paranthropus* and *Plesianthropus*, Broom indicated that the large cranial capacity and sagittal crest of *Paranthropus*, along with the differences in pelves and deciduous anterior dentition were enough to warrant such a split.

The following year Broom and Robinson produced the last of their monographs on the australopithecines, this one dealing with *Paranthropus crassidens*. Again this volume gave excellent anatomical descriptions of the known fossil materials of both *Paranthropus crassidens* and *Telanthropus capensis*. In the discussion of the affinities of *Paranthropus crassidens*, much mention was made of the difficulty in ensuring that fossils are properly placed within correct genera and species, and the possibility of errors being made in paleontology. Mention was also made of the fact that many researchers at the time of the South African fossil discoveries were rather reluctant to accept not one but three genera of such morphologically similar anthropoids, namely *Australopithecus*, *Plesianthropus*, and *Paranthropus*. Broom rebutted this argument by stating that "we do not publish all our evidence. But this does not mean that we make new species and genera without the strongest evidence (Broom and Robinson, 1952:97)." However, he went on to assert that since the supposed geological age of the sites was different, it was "highly probable that the ape-men of the deposits were very different species and even genera (Broom and Robinson, 1952:97)."

Again, Broom's main criteria in separating out different genera was the relative geological age derived from faunal associations. And again, the different geological ages were based on the fact that different faunas were found at the different sites. Mayr made an excellent point regarding this idea though, stating that "contemporary modern man can be found associated with okapis or elephants or tigers or kangaroos, or South American edentates or with polar bears (Mayr, 1950:113)." The point of this statement was that different faunas do not necessarily indicate different ages or different genera. Broom's justification for naming new genera for almost every South African site, both morphologically and geologically, was rather weak.

Discussing the new finds that were made at Swartkrans, Broom indicated that, even though *Paranthropus crassidens* was initially named on only two lower premolars and three lower molars, subsequent fossil finds proved the specific distinction is valid (without saying how). Further, Broom added that when *Paranthropus robustus* became better known, it might be necessary to erect a new genus for *Paranthropus crassidens*. All this was noted in spite of the recent work by men such as Ernst Mayr and Le Gros Clark to halt the unnecessary proliferation of invalid nomina in human paleontology, and to seek a clearer understanding of the true nature of the relations between the species of australopithcines. Taxonomic categories should no longer be used (then or now) as vehicles for fame, funding or devices of convenience. Firm biological meanings should be attached to each new name, with firm biological bases, rather than just arbitrary sorting of long lists of traits into "best fit" categories.

When it came down to the actual taxonomy of the Hominidae, however, not all were convinced of the reality of the many nomina that had been erected. In one of the first efforts to deal with the generic status of the australopithecines, Washburn and Patterson indicated that "the family [Hominidae] might conveniently be divided into two genera, *Australopithecus* and *Homo* (Sherwood and Patterson, 1951:651)." Here was one of the earliest attempts to reduce the taxonomic overburden that had accumulated over the years, and many subsequent authors found great significance in these words.

The final event of this section of the early history of human paleontology is the culminating event that allowed the proper analysis of the African fossils to begin. The exposure of the Piltdown fraud removed this final obstacle from the path of legitimate scientific enquiry, and allowed the South African fossils to assume the position they deserved as our own human ancestors. The Piltdown hoax was officially revealed in 1953 by Joseph Weiner, Kenneth Oakley, and Wilfrid E. Le Gros Clark. Although this was the first revelation of the fraud, its actual intricacies were not fully revealed until 1955 when even more complete analyses were performed on the Piltdown remains. Joseph Weiner in 1955 laid bare all the bones of the Piltdown deception, and laid to rest forever what has been called the greatest hoax ever perpetrated in science.

It became evident in approximately 1953 to Weiner that there was a great likelihood of the Piltdown materials having been deliberately forged. It was noted that the teeth of the Piltdown mandible were worn in an unusually flat pattern, one that had suggested a human pattern of wear. Upon closer analysis it could be seen that the teeth were actually worn perfectly flat, a condition not seen in humans. Also, the degree of wear of the 1st and 2nd molars was identical, even though the 1st molar would have erupted much earlier than the second. Weiner realized that the only detail of the mandible that made it appear human and not ape was this very wear. He further realized that the exact diagnostic areas of the mandible, those which could settle its ape vs. human affinity, such as the condyles and the chin region, were conveniently missing. Together with Oakley and Le Gros Clark, he attempted to create his own fake fossils, and was quite successful at it. The three then published their findings in 1953, and indicated that the mandible and skull were not of the same creature, and that the mandible had been very likely artificially manufactured.

Following this article, a whole battery of tests was performed on both the mandible and skull. Oakley had tested the Piltdown materials for fluorine content, and it was discovered that not only were they apparently of different ages, but they were also geologically rather recent. They next tested the fossils for iron, nitrogen, collagen, organic carbon, organic water, radioactivity, and crystal structure. All these tests showed that the skull and mandible did not belong together, and that they were of relatively recent ages. It was soon determined that a modern orang-utan jaw and a human cranium, as well as some isolated teeth, had been artificially stained and altered to give the appearance of great age. It became apparent that an elaborate hoax had been perpetrated, and that the scientific establishment had been thoroughly fooled by it.

With the final debunking of the Piltdown forgery, the way was at last open for a proper understanding of human evolution to be achieved. The South African fossils were finally accepted for the human ancestors they were, and it was realized that the prevailing belief of anthropologists that brain expansion was the hallmark of humanity was finally put to rest. As Tobias indicated, "it would be no exaggeration to claim the the Piltdown fraud and Keith's avid espousal of the Piltdown remains held up the advance of paleoenthropology for a quarter of a century (Tobias, 1992:260)." When this holdup was removed, the field of human paleontology changed forever.

2.3 The Middle Period 1953-1978 - The Lumping Trend

After the exposure of the Piltdown forgery, a new avenue was opened for a more realistic understanding of human evolution to take place. The true nature of our pre-human ancestors began to emerge in the form of the australopithecines. Small-brained, diminutive, erect walking bipeds, rather than large brained, ape-bodied primates were our direct lineal ancestors. One of the first aims of human paleontology after this event was to clarify the taxonomy of the australopithecines. It had been noted by many that considerable confusion typified the field owing to the unclear relationships between the species and genera recognized at the time (once again we must remember that fossil sites equaled species).

An early attempt at clarification was made by Ernst Mayr as noted in the previous section. However, most paleoanthropologists were unwilling to accept such an extreme lumping. Middle ground was required. Another early attempt was made by Washburn and Patterson, who suggested that the Hominidae might be comfortably divided into two genera, *Australopithecus* and *Homo* (Washburn and Patterson, 1951:650-651). This suggestion was well met, and the morphological groundings for such a move were sought, especially following the debunking of Piltdown.

John Robinson was one of the driving forces behind the lumping trend of the early 1950's. With the ever expanding fossil hominid catalogue came an understanding of the amount of variation exhibited by the different species. It was becoming apparent that there was a significant amount of over-classification within the australopithecines, and that many of the recognized genera and species could quite comfortably fit within other already existing genera and species. Beginning in 1953, Robinson undertook the great task of re-analyzing all the known South African fossil species, and uncovering their true phylogenetic relationships. As a result, most of the known hominid taxa were sunk, and their hypodigms referred to other species.

Robinson was one of the first to attempt to codify what he saw as a major distinction between two groups of fossils. He labeled the two groups prehominids and euhominids. The prehominids were essentially the australopithecines. In 1953 the distinction between *Plesianthropus* and *Australopithecus* was still widely held, and along with *Paranthropus*, they made up the prehominids. The euhominids, or true hominids, were those species considered to be on the direct line to humans, those which shared numerous morphological features with humans. The euhominids included all members of the genus *Homo*, as well as *Pithecanthropus*, *Sinanthropus*, and *Telanthropus*, all of which would eventually be referred to the species *Homo erectus*.

Robinson first attacked the new hominid species that had just been named by Weinert in 1951, *Meganthropus africanus*. This species had been named on the strength of one single incomplete (and damaged) mandible found at Laetolil in Tanzania (Weinert, 1950). It had originally been named *Praänthropus* by Hennig (1948), but no specific name had been given. Weinert had subsequently referred the material to *Meganthropus*, with the new species name, *africanus*. Robinson believed that based on all the morphological evidence the mandible provided "it [was] apparent that the characters of *Meganthropus africanus* may all, as far as they are at present known, be found among the australopithecines" (Robinson, 1953a:8). He felt there was no reason to refer the new mandible to *Meganthropus*, the same genus which housed certain Javanese fossils in the species *M. palaeojavanicus*. Between *M. africanus* and *Plesianthropus transvaalensis* Robinson felt there were no distinguishing features which could differentiate the two, nor were there any between *M. palaeojavanicus* and *Paranthropus crassidens*. He was certain that the fossils of *Meganthropus* were australopithecines; they were prehominids. The generic distinction between *Meganthropus* and the australopithecines was maintained because at the time Robinson felt that further fossil finds might warrant it, and rather than confuse the issue he left the taxonomy intact for the time being.

Later that same year Robinson took to discussing the affinities of the euhominid material from Swartkrans, *Telanthropus capensis*. He felt this taxon was a transitional form between the prehominids and the euhominids, though he also certainly considered it to be an euhominid. He discussed its relationships to various other euhominids such as *Pithecanthropus* and *Sinanthropus*, and mentioned the possibility that *Telanthropus* might actually belong to the same genus as *Pithecanthropus* (Robinson, 1953b: 499). In actuality, they both belong to the species *Homo erectus*, as would be proven in time. As something of a side note, in the same article he stated that "in passing it may be noted that *Plesianthropus* is most probably a synonym of *Australopithecus* which would then include the specimens from Taungs, Sterkfontein, and Makapan (Robinson, 1953b:492)."

Robinson elaborated on this point in the following year in an extremely important article wherein he rewrote early hominid taxonomy. He formally sank *Plesianthropus*, referring all its material to the genus *Australopithecus*. He also sank *Meganthropus*, referring all its material to *Paranthropus* (Robinson, 1954: 198). *Australopithecus prometheus* was sunk in favor of *Australopithecus africanus*, and relegated to the status of subspecies. The same was done for the trivial name *transvaalensis*, which, again, was given subspecific rank in *Australopithecus africanus*. The taxon *Paranthropus crassidens* was referred to *Paranthropus robustus*, again with a subspecific rank. *Paranthropus palaeojavanicus* maintained a specific distinction from *Paranthropus robustus*, owing in part to the extreme geographical separation of the two (*Paranthropus palaeojavanicus* designated the fossils found in Java). A generic distinction was maintained between *Australopithecus* and *Paranthropus* because Robinson felt the two were sufficiently different both morphologically and ecologically that they represented very different lines of evolution.

Remane argued against Robinson's placement of *Meganthropus* within the australopithecines, saying "the resemblences with the South African hominids *Plesianthropus*, *Australopithecus* and *Paranthropus* are not very distinct (Remane, 1954:125)." He further asserted that the attribution of the Laetolil fossils to the genus *Meganthropus* (trivial name *africanus*) was valid based on the maxillary premolars, even though *Meganthropus palaeojavanicus* (the Javan species) possessed only mandibular premolars. He noted the fact that there were no comparable teeth between the two sets of fossils, located thousands of miles apart, yet still confidently placed the two in the same genus.

Rebutting Remane, Robinson reiterated that the *Meganthropus africanus* specimen found at Laetolil in Tanganyika fit quite well within *Australopithecus africanus* (though further finds might have required a specific distinction), and that the *Meganthropus palaeojavanicus* materials belong within the genus *Paranthropus*. He again pointed out the fact, noted by Remane, that there were no comparable teeth between the two claimed species of *Meganthropus*, therefore the association of the two was at best quite tenuous (Robinson, 1955:429).

Adding to the debate on the taxonomic position of *Meganthropus africanus*, Senyürek discussed the various attributions it had received previously. He agreed with Robinson that the teeth found at Laetolil did not belong in the genus *Meganthropus*, and that they were, in fact, australopithecines. However, he felt that ". . . the differences which distinguish the Serengeti maxilla, labeled as *Meganthropus africanus* by Weinert, from *Paranthropus* and *Australopithecus* entitle it to a separate generic rank . . . [and] I propose to rename this maxillary fragment from the Serengeti district as *Praeanthropus africanus* (Senyürek, 1955:33)." The morphology of the teeth was, to Senyürek, closer to the australopithecines than to *Meganthropus*, but *Praeanthropus* was not on the direct ancestral line to *Homo*. This new designation was never well received, and died a quick death owing to neglect.

As had long before begun to typify the field, there was strong disagreement over the taxonomic scheme proposed by Robinson. Oakley (1954; 1956) objected to the recognition of three genera within the Hominidae, preferring Washburn and Patterson's (1951) system which recognized only *Australopithecus* and *Homo*, excluding *Paranthropus*. Dart as well rejected Robinson's multiple taxa, stating that ". . . a single australopithecine genus could provide sufficient species to include all the known South African forms (Dart, 1955:71)." Regarding *Telanthropus capensis*, Dart felt, along with Le Gros Clark, that ". . . the *Telanthropus* specimens are in fact, australopithecine, there is nothing sufficiently distinctive in the palate to separate it even specifically from *Paranthropus* much less to divorce it generically or familially from its geological contemporary (Dart, 1955:72)." He felt they were conspecific with *Australopithecus (Paranthropus) crassidens*.

Other North African finds (aside from *Meganthropus*) were being made at this time as well. Arambourg and Hoffstetter announced the discovery of two mandibles in Algeria, at the site of Ternifine, one of which possessed a complete dental arcade (1954:73). It was found associated with stone tools, and was referred to the middle Pleistocene. Later that same year, a name was given to the new find, *Atlanthropus mauritanicus* (Arambourg, 1954:895). It was compared to both *Pithecanthropus* and *Sinanthropus*, and though it was called a Pithecanthropine, a new taxon was erected to accommodate it. Eventually, however, its status would be relegated to a member of the species *Homo erectus*.

In 1956 Robinson produced another of the extremely valuable Transvaal Museum series, this time on the dentition of the australopithecines. In it he performed an exceptionally detailed analysis of all of the known australopithecine fossils, comparing them to other known hominid fossils like *Sinanthropus* and *Pithecanthropus* (Robinson did not believe these genera to be taxonomically valid, but rather utilized the names as a matter of convenience). One of his main conclusions was that the distinction between *Australopithecus* and *Paranthropus* was in fact morphologically and ecologically valid. In opposition to the earlier works that had been produced, Robinson spent very little time attempting to differentiate the australopithecines from the apes, concentrating instead on comparisons with the known euhominids. The main purpose was to outline the differences and similarities between the prehominids and the euhominids, as well as delineate the main morphological differences between *Australopithecus* and *Paranthropus*.

Robinson also further developed his ecological reasoning for separating out *Australopithecus* and *Paranthropus*. He felt that *Paranthropus* represented a strictly vegetarian animal, and this reliance on extremely involved mastication was responsible for the 'robustness' of many of their traits. The teeth were large with well developed enamel and firm roots, all of which point to extensive grinding and crushing. The small canines were of apparently little use to these early hominids. The large masticatory apparatus required large masticatory muscles and a strong bony face to withstand the pressure of the chewing forces. Sagittal crest formation accompanied such an enhanced food processing mechanism, as did large facial structures like huge zygomatioc arches and bony buttresses. Robinson felt that these were clearly very specialized chewing animals, similar in many respects to the gorilla (Robinson 1956:170).

Australopithecus on the other hand, was a smaller, more omnivorous creature, which was apparently much closer to the euhominid stage than was *Paranthropus*. The lessened need for such a heavy duty chewing apparatus was the determining factor in the smaller, more 'gracile' form of the skull of *Australopithecus*. It was thought that hunting and meat consumption played a much more important role for *Australopithecus* than for *Paranthropus*. When again discussing the morphological differences between the two australopithecine genera, Robinson noted that "the differences between the two are of such magnitude that separate generic status is a necessity even from a conservative viewpoint. There is greater difference between them than between the gorilla and the chimpanzee" (Robinson, 1956:171). It is precisely this magnitude of difference that this thesis intends to test, and it will be determined if Robinson was in fact correct on this point in subsequent chapters.

At the same time that the controversy was raging over the South African material, new finds were being made in Asia. In 1957 von Koenigswald described what he apparently felt to be a new type of fossil hominid from China. He named his new taxon *Hemianthropus peii*, and commented on its close likeness with *Paranthropus* (von Koenigswald, 1957:158). He stated that the new species was ". . . a higher primate of subhuman affinities (probably not closer related to the Australopithecinae) rather than a true member of the Pongidae (von Koenigswald, 1957:158)." It would appear that he felt it to be different from the pongids, but not a true human ancestor, an australopithecine.

As mentioned in the last section, another of the great driving forces in the new understanding of hominid evolution was Le Gros Clark of Oxford. His anatomical analyses of the australopithecine materials were precise and thorough, and the conclusions he reached are still useful and valid today. In 1955 he published another major work in human paleontology, entitled *The Fossil Evidence for Human Evolution*. The first chapter of the book was dedicated to the uncovering of many of the problems inherent in human paleontology. Le Gros Clark stressed that the total morphological pattern of fossils must be studied, not just isolated differences (Le Gros Clark, 1955:12). This is the direction this current study is undertaking, namely to look at *all* morphological criteria used in the past to define the australopithecine species, and to consider them all together as part of single coherent taxa.

Le Gros Clark also noted the fact that when the fossil record of a group of primates is small and fragmentary, the proper amounts of group variability cannot be properly assessed until more fossils are known (Le Gros Clark, 1955:15). As more material becomes available, the taxonomy of that group may require revision. Essentially, he noted what this current chapter is underlining, the early splitting trend within a field, and its subsequent lumping as more fossils become known and the variation within that group is made apparent. Le Gros Clark was a strong advocate of the lumping of the australopithecines into more phylogenetically realistic groups. As proof of this point he referred to the South African fossils, and the fact that though Broom had named 3 genera and 4 species, few accepted them as being valid, owing to the increases in intraspecific variation being noted with the new fossils. Le Gros Clark felt, along with others, that the case for generic distinction between the groups was not strong.

Of extreme importance to this study is the suggestion of Le Gros Clark that "paleoanthropologists, by an international convention, should agree to refrain from creating any new species or genus on the basis of a fossil specimen unless it can be demonstrated with reasonable assurance that the skeletal and dental characters of the specimen deviate from those already known *to an extent at least equivalent to the differences between recognized species or genera* *in recent representatives of the same or allied groups* (1955:16; italics mine)." It is precisely this outgroup comparison which will here be performed with closely allied groups, the chimpanzees and gorillas. Unfortunately, this sage advice was not often heeded, and many new species and genera were named (though not all were accepted), all the way until 1986 when a new species *Australopithecus aethiopicus* was named based entirely on a cladistic analysis of one single skull.

The taxonomic relevance of characters used to define species was of great importance to Le Gros Clark as well. He noted that "each natural group of animals is defined . . . by a certain pattern of morphological characters which its members possess in common and which have been found by the pragmatic test of experience to be sufficiently distinctive and consistent to distinguish its members from those of other related groups (Le Gros Clark, 1955:20)." The pragmatic test that he is referring to is precisely what is being attempted here. The use of morphological characters to distinguish between australopithecines is here compared to extant apes to test their taxonomic validity. This study will serve to highlight exactly which australopithecine character traits actually define the taxa as being different from others, and which do not.

In a subsequent work, Le Gros Clark pointed out what he felt was the most important confounding variable in the study of human evolution, which was ". . . the tendency for the taxonomic individualization of each fossil skull or fragment of skull by assuming it to be a new type which is specifically, or even generically, distinct from all others (Le Gros Clark, 1958: 3)." He felt such spurious namings were unnecessarily confusing the picture of human evolution. Although this criticism was directed at researchers of the day who named a new species for each find, it applies equally well to those today who would see new species based on single or scanty remains (e.g., *Australopithecus aethiopicus*), or on perceived statistical differences (e.g., *Homo rudolfensis*, *Homo ergaster*). To Le Gros Clark, there was "no morphological basis for recognizing . . . more than one genus [of Australopithecine] (Le Gros Clark, 1958:4)" in 1958. He also doubted the generic distinction between *Australopithecus* and *Telanthropus*, noting the close similarities between the two (*Telanthropus* was incidentally sunk within *Homo erectus*, thus showing the close relationship the two hominid genera share).

Further criticizing the taxonomic overabundance of the Hominidae, Le Gros Clark stated that ". . . it is an interesting but not generally recognized fact that practically none of the genera and species of fossil hominids which have from time to time been created have any validity at all in zoological nomenclature (Le Gros Clark, 1958:6)." Time heals all wounds, and sinks most taxa. Of the many species named since Le Gros Clark made this statement, only two (*Australopithecus [Zinjanthropus] boisei* and *Australopithecus afarensis*) have achieved widespread (though by no means complete) acceptance. Others including (but not restricted to) *Tchadanthropus uxoris* and *Paraustralopithecus aethiopicus* have fallen by the wayside. Whether the two accepted taxa are valid indeed is the subject of this thesis.

The overburdened taxonomic status of the australopithecines also caught the eye of certain zoologists who felt it necessary to comment on topics outside their field. Ernst Mayr (1950) was the first to provide a discussion of the problem, but others followed his lead. Brown (1958) agreed with Mayr that all fossil hominids could be comfortably housed within one genus. He went further and stated that "in comparison with other zoological fields, physical anthropology leans heavily upon the genus to distinguish its finds, and one might even say that, allowing for a clearly excessive synonymy, the anthropological genus is more or less equivalent to the zoological species (Brown, 1958:151)." His solution was to substitute the generic name for the specific name, and subsume all within the genus *Homo* (e.g., *Homo meganthropus* or *Homo australopithecus*). His less radical (and perhaps less facetious) recommendation was one that had been communicated to him by Mayr. Mayr had suggested that all of the australopithecine generic names should be considered synonyms of *Homo*, but that they could be retained in the vernacular to refer to the fossils. This was the stance that Brown adopted.

The relationship between the australopithecines and modern humans was at the time (the late 1950's) still not fully understood. In a discussion about the dentition of hominid fossils, von Koenigsvald indicated that he believed that the australopithecines were a lateral branch on the phylogenetic tree, and not ancestral to modern humans (von Koenigsvald, 1958, in Howells, 1962: 306). When he looked at the generic status of some of the fossils, he concluded that *Meganthropus* could not be closely allied to

Paranthropus as Robinson felt, due to the root pattern of the second premolar (among other unstated features). Regarding the australopithecines themselves, he stated that "since it is possible to classify the australopithecines according to the degree of molarization of the first deciduous molar. . . it is hardly to be doubted that they all belong to the same genus (von Koenigsvald, 1958, in Howells, 1962:304)." He also felt it was preferable to keep all the old species names to distinguish the fossils according to their deposits; again, taxonomy as a convenience.

For Emil Breitinger, there was no question whatsoever that the australopithecine fossils represented hominids. The pelvis of *Australopithecus africanus* from Sterkfontein allowed for the positive conclusion that these animals had walked bipedally, and since this was considered to be the most decisive factor in defining humans, australopithecines must be closer to the human than the pongid condition (Breitinger, 1959 in Howells, 1962:186). Analysis of the skull and dentition of the australopithecines further strengthened this conclusion. Breitinger felt that *Australopithecus* deserved at least a generic distinction from *Homo*. He also agreed that other genera such as *Sinanthropus* and *Pithecanthropus* did not (they belonged to *Homo erectus*). He remained uncommited on the issue of whether or not *Australopithecus* was a human ancestor; it was entirely possible if they were determined to be old enough geologically.

The geological age of the australopithecines appears to have been a major stumbling block for their acceptance into the human lineage. Heberer felt, as did many at the time, that because of their supposed geological recentness, the australopithecines were too young to have been direct human ancestors (Heberer, 1959, in Howells, 1962:236).

Discussing taxonomy, Howell was able to conclude that although the australopithecines were "usually classed as a distinctive subfamily (Australopithecinae) of the Hominidae, [they] quite probably represent merely a distinct genus, *Australopithecus*," and that "the group contains two probably subgenerically distinct forms, *Australopithecus* and *Paranthropus* (Howell, 1959: 836)." He went on to outline many of the morphological differences that separated the australopitheinces from the apes, as well some of the differences that separated what he saw as two subgenera, *Australopithecus* and *Paranthropus*. Discussing *Telanthropus*, he made mention of the fact that it very closely approached the phylogenetic status of other forms attributed to *Homo*, although he reserved final judgment on this issue until more and better fossils were known of the taxon.

The year 1959 was a significant one in the field of human paleontology, because it was in that year that Olduvai Gorge entered the scene with its first major fossil hominid contribution. The indefatigable Louis Leakey announced the discovery, made by his wife Mary,. of an extremely well preserved skull of what he felt to be a new genus of early hominid. He named his new find *Zinjanthropus boisei*, and he listed out a whole suite of morphological characters that he felt defined his new species. He indicated first that although in South Africa "some scientists recognize only one genus, namely, *Australopithecus*, and treat Broom's *Paranthropus* as a synonym; others consider that the demonstrable differences are of such a nature that both genera are valid. Personally, having recently re-examined all the material of the two genera, in Johannesburg and Pretoria, I accept both as valid (Leakey, 1959: 491)."

What Leakey was saying was that he felt the differences in morphology of the australopithecines were sufficient to warrant the generic distinction. He further felt that his new find was different enough that it too required a generic distinction. This view of his was later defended by Simpson who stated that ". . . when Leakey inferred from an Olduvai specimen . . . the existence of a taxon that he called *Zinjanthropus boisei* he was using correct taxonomic grammar to express the opinion that the taxon was distinct at both specific and generic categorical levels from any previously named (Simpson, 1963:5)." Although *Zinjanthropus* is now considered invalid (i.e. that it was overclassified), Leakey was still correct in his methodology. He believed that his new skull differed more from *Australopithecus* and *Paranthropus* than either did from each other. The validity of the new genus, however, was instantly challenged.

Robinson immediately attacked Leakey on the designation of the new genus. He indicated that many of the traits Leakey described were too brief to use for comparison, while others were simply the result of the new skull being significantly larger than any known australopithecine at the time, and were therefore only size differences (Robinson, 1960:456). The remaining points Leakey had listed were then analyzed one by one to determine the true affinity of the new skull. Robinson reiterated his view that the differences between *Australopithecus* and *Paranthropus* were mainly dietary. *Australopithecus* was a meat eating genus, with larger anterior dentition and smaller molars, while *Paranthropus* was predominantly a vegetarian, with reduced anterior cutting teeth and extremely large grinding molar teeth. The grinding forces required to undertake the significant amount of chewing *Paranthropus* did caused the modifications seen in the skull architecture that lead to the extreme robustness of the OH5 skull from Olduvai, as well as the extreme development of the areas of muscle attachment, namely the crests. The features of the new *Zinjanthropus* skull fit this pattern quite well. Robinson recommended that the generic name *Zinjanthropus* be dropped in favor of *Paranthropus*, but that the specific name *boisei* be kept for the moment as the true specific status could not be determined from one skull only (Robinson, 1960:458).

Leakey made an immediate reply to these criticisms by first of all stating that he did not wish to get into a protracted taxonomic debate over *Zinjanthropus* since it was ". . . purely a question of artificial labels" anyway (Leakey, 1960:458). He stated that the ". . . very considerable work I have done on the *Zinjanthropus* skull since my preliminary report in *Nature* has greatly strengthened my view that it is entirely different from *Australopithecus* and *Paranthropus*, differing from both these genera more than they do from each other (Leakey, 1960:458)." The similarities noted by Robinson between *Zinjanthropus* and *Paranthropus* were dismissed by Leakey either by reiterating the original point made or by stating a difference existed with little discussion as to details. Leakey was waiting for the much more comprehensive report of Tobias (1967b) on the morphology of the skull to come out. Presumably this monograph would settle all questions, and will be dealt with below.

The finds at Olduvai continued to accumulate, and it was in 1960 and 1961 that some of the most remarkable ones were made. A mandible, two parietal bones, and a partially complete cranium were found which bore many resemblences to both Pithecanthropines and modern humans (Leakey, 1961a:650). The ages of the deposits that these fossils came from were finally fixed at approximately 1.75 Myr old (Leakey, et al. 1961:479). For the first time, newly developed radiometric dating techniques could be applied to the early hominid fossils.

When more teeth were known from Olduvai, it became possible to compare their sizes with those from South Africa. Leakey noted that the third and fourth lower premolars of *Zinjanthropus* were longer than they were wide, while for *Australopithecus* and *Paranthropus* they were wider than they were long (Leakey, 1961b:417). The fact that morphological differences existed was also noted, though what these differences were was not elaborated upon. The index (100xLength)/Breadth of the first and second molars was shown to fall outside of the range of variation for *Australopithecus* and *Paranthropus*, and again, unspecified morphological differences were noted for *Zinjanthropus* (Leakey, 1961b:418). Based on these dental differences, Leakey felt he had successfully defended the generic status of *Zinjanthropus*.

Leakey's ideas about the actual taxonomic position of *Zinjanthropus* was made quite clear in 1963, when he stated that he was convinced that neither *Zinjanthropus*, nor any of the australopithecines of South Africa, were ancestral to *Homo*. He alluded to the presence of a more advanced hominid at Olduvai, which he felt was much closer to 'hominine' status than any of the other fossils, resembling *Pithecanthropus* closely (Leakey, 1963:456). He felt these discoveries would change our understanding of human evolution, and though he was correct on this point, it would not be in the manner he expected.

Regarding the taxonomic status of *Zinjanthropus* itself, Leakey stated "I fully realize that the question of whether these differences justify generic, or only specific, differentiation, is one which depends upon point of view, but I believe that *Zinjanthropus* differs as much (or more) from the South African genera as gorilla does from chimpanzee (Leakey, 1963:455)." I couldn't have said it better myself, and it is exactly this magnitude of difference that this current study will test. In spite of Leakey's assurances, many were not swayed as to the generic distinction of *Zinjanthropus*, and as we shall soon see, his final assessment was shown to be in error.

The existence of *Zinjanthropus*, although accepted by some, was never truly approved by the scientific community. Robinson never allowed it a place in hominid taxonomy. He considered it to be merely a member of the genus *Paranthropus*. He was also reluctant to accept any other new nomina in the 1950's and 1960's, arguing quite effectively against *Präanthropus* Hennig (a *nomen nudum* as no trivial name was given) and *Meganthropus* Weinert, which he considered to be *Paranthropus* (Robinson 1963:397). He would allow only *Australopithecus* and *Paranthropus* into the Hominidae as ancestors, claiming a distinct morphological and ecological difference between the two forms. He further reduced the ancestral roster to *Australopithecus* only, claiming that *Paranthropus* was far too specialized as a dedicated vegetarian to qualify as a last human ancestor (Robinson, 1963:405). One interesting note is that at this time Robinson felt that *Paranthropus* was the older of the two genera, that it had given rise to, and was subsequently driven to extinction by, *Australopithecus*. The ages of the South African sites were not then very well known (nor are they today).

By a similar token as above, the distinction that Robinson saw between *Australopithecus* and *Paranthropus* was not accepted by all. The great geneticist Theodosius Dobzhansky recognized only the genus *Australopithecus*, accepting 3 species, *A. africanus*, *A. robustus*, and *A. boisei* (Dobzhansky, 1963:356). Harrison and Weiner felt that "the contrast between [*Australopithecus*] and *Paranthropus* is considerable (1964:63)," but that "the differences between all these South African remains seem to be no greater than those which occur within other accepted genera of hominids, and only the single genus *Australopithecus* is here recognized, albeit with two species, *Australopithecus africanus* and *Australopithecus robustus* (*'Paranthropus'*) (Harrison and Weiner, 1964:64)."

Discussing *Zinjanthropus*, Harrison and Weiner felt that the fossils discovered were very like *Australopithecus robustus*, and that they too should be included within the genus *Australopithecus*. Although they did not directly discuss the specific status of the Olduvai material, they apparently felt that the *Zinjanthropus boisei* specimens should be included within *Australopithecus robustus* (Harrison and Weiner, 1964:64). Hulse agreed with this, stating that "no valid taxonomic reason can be found for assigning a separate generic name to *Zinjanthropus*" and that "all of these forms should be thought of as representatives of the same genus and perhaps the same species (Hulse, 1963:191)."

Others as well accepted the view that there was only one fossil hominid genus, *Australopithecus*, again with only two species, *A. africanus* and *A. robustus* (Campbell, 1963:67). Campbell did not include Leakey's *boisei* species, choosing to await a more detailed analysis. Campbell went further and claimed that *Meganthropus africanus* and *M. palaeojavanicus*, as well as *Telanthropus capensis* were also sunk into *Homo erectus* (Campbell, 1963:70). He indicated that in the past at least 105 species had been named in the family Hominidae, 63 of which were invalid by the rules of zoological nomenclature (Campbell, 1963:69). Of the remaining species, all but 4 were sunk at some point in the past, leaving only *Australopithecus africanus*, *Australopithecus robustus*, *Homo erectus*, and *Homo sapiens*. Truly a monumental tribute to taxonomic overabundance.

Pilbeam and Simons as well contested the existence of *Australopithecus boisei*, claiming "we believe that it cannot be distinguished at the specific level from *A. robustus* (Pilbeam and Simons, 1965:248)." *Telanthropus capensis* was presumed to belong to the genus *Homo*, although they were unclear on the specific status, stating that if the taxon was referred to *Homo*, the trivial name *capensis* would not have priority as *Homo capensis* was previously used by Broom to name the Boskop finds in 1914. The validity of the taxon *Homo habilis* (discussed below) was also not accepted as proven, and the suggestion was even made that *Australopithecus* might be sunk within *Homo*, creating *Homo africanus* to accommodate the 'gracile' early hominids (Pilbeam and Simons, 1965:257).

Others preferred to await further fossil finds before making a final decision. Mayr felt that the decision between accepting one australopithecine genus or two was essentially a matter of taste, and that he would wait for new finds to help resolve the situation (Mayr, 1963:342). When he spoke of the separation between *Australopithecus* and *Homo*, however, he recanted his 1950 position that they belonged within one genus. He felt that "the extraordinary brain evolution between *Australopithecus* and *Homo* justifies the generic separation of these two taxa, no matter how similar they may be in many other morpholgical characters (Mayr, 1963:341)." Still, the improvement of the classification of the Hominidae from a merely typological stance to one recognizing population diversity was the most important factor that allowed a much more realistic understanding of human evolution to take place, according to Mayr.

The next great taxonomic bombshell to be dropped came in 1964 when Leakey et al. described what they felt to be a new species of the genus *Homo*, which they called *Homo habilis*. Of more direct relevance to this study is the fact that the authors also rewrote the taxonomy of the australopithecines again. Following Clark's (1955) definition of the family Hominidae, they "accept[ed] the genus *Australopithecus* with, for the moment, three sub-genera (*Australopithecus*, *Paranthropus*, and *Zinjanthropus*) and the genus *Homo* (Leakey, et al., 1964:7)." They also formally regarded *Pithecanthropus* as a member of the genus *Homo*. A mere five years after it was named, the genus *Zinjanthropus* was sunk, this time by its own author, in favor of a clearer and more realistic picture of human evolution.

The diagnosis of the genus *Homo* was reassessed by the authors in light of the new species they were naming, to allow it a more comfortable fit. A great deal of controversy surrounded the new species, and many refused to accept it as valid. This discussion is beyond the scope of the present study, and as such, the controversy, and the various arguments pro and con, will only be briefly summarized, with no attempt at analysis.

The following year John Robinson took issue with *Homo habilis*, claiming it was not valid both on morphological and nomenclatural grounds. Strictly taxonomically speaking, the rules of the International Code of Zoological Nomenclature (ICZN) were violated when Leakey et al. stated that their find might be conspecific with *Telanthropus capensis*. This would make *capensis* rather than *habilis* the trivial name as it was the senior published nomen. Robinson also pointed out that the revision of the genus *Homo* which was performed was based on prior acceptance of the new species, although the proof of its validity appeared to be entirely lacking (Robinson, 1965b:121). Robinson claimed that the new species was based on only a few morphological differences of uncertain taxonomic valence. Particularly, the dental characteristics were important to Robinson, and he showed that the teeth of *Homo habilis* fell within accepted ranges of variation for the known australopithecines (Robinson, 1965b:122). Beyond simply falling within accepted ranges of variation, however, Robinson pointed out that such morphological features were of low taxonomic valence, noting that "the intra-species variation in the mean in modern man is actually greater than the intergeneric differences in the mean for three populations of *Australopithecus*, *Paranthropus*, and *Homo erectus* (Robinson, 1965b:122)." Dental modules to Robinson were of little taxonomic use.

The fact that the type and paratype specimens for the new taxon came from two different Beds at Olduvai also did not escape the attention of Robinson. He felt that "it is . . . by no means clear that the Bed I and Bed II groups of specimens necessarily belong to the same species (Robinson, 1965b:123)." Instead, he preferred to place the Bed I materials within *Australopithecus africanus*, and the Bed II materials within *Homo erectus*. He felt there was more reason for associating the fossils thus than there was for associating them with each other. It appeared as though the Bed I material was ancestral to the Bed II fossils, and that the two groups represented a single lineage, with the Bed I individuals evidencing a transitional stage between the two genera *Australopithecus* and *Homo* (Robinson, 1965b:123).

Robinson even went so far as to suggest that the genus *Australopithecus* be absorbed within *Homo*, as he felt it was very clear that a direct ancestor-descendent relationship existed between the two (Robinson, 1961, 1965b, 1968, 1972). *Paranthropus* would remain as a valid external genus of highly specialized herbivores, not on the direct line to modern humans. This closely matched the recommendation Mayr had made in 1950, but as we saw above, Mayr had recanted this position, leaving Robinson alone to pursue this line of reasoning. The specific status of the newly expanded genus would also require revision, and Robinson recommended that *Homo transvaalensis* be created to accept all small brained tool users, while *Homo sapiens* would include all large brained tool makers. Although interesting, this idea never received wide acceptance.

Tobias replied to Robinson's criticisms the following year, claiming that, in fact, the dental differences seen in *Homo habilis* were significant. He criticized Robinson for the inappropriate inclusion of one incompletely formed tooth which altered Robinson's outcome significantly. Answering one other of Robinson's challenges, Tobias noted that the Bed II material had been removed from *Homo habilis*, and was considered to be a more advanced form of hominid (Tobias, 1966:954). The *Homo habilis* teeth with no uncertainty showed a narrowing trend when compared with the australopithecines. The internal mandibular contour of the OH7 type mandible also supported the new species, contrary to what Robinson claimed. As well, Tobias showed that the L/B index Robinson had stated to be of low phyletic valence, was in fact able to distinguish between some hominid taxa. Looking next at Robinson's suggestion that *Australopithecus* be sunk within *Homo*, and *Paranthropus* remain valid, Tobias noted that most researchers at the time accepted *robustus* as belonging to *Australopithecus*, recognizing no generic distinction. Robinson's claim was based mainly on inferred ethology, and it would be rare to see such evidence outweigh the morphological evidence that placed *Paranthropus* and *Australopithecus* in the same genus (Tobias, 1966:956).

Replying to Tobias' reply, Robinson claimed that the internal mandibular contour Tobias supplied actually enhanced his

(Robinson's) claim that it was more australopithecine. Regarding the cranial capacity, Robinson again claimed that the value obtained for *Homo habilis* (based on two isolated and incomplete parietals) could still fit within the range of variation allowable for *Australopithecus*. Robinson further rebutted Tobias' claim that he used ethological evidence over morphological, claiming that his separation of *Paranthropus* and *Australopithecus* was based upon morphological differences (Robinson, 1966:958). His behavioral interpretations were also based on morphological criteria (e.g., extreme vegetarianism based on large grinding teeth, large temporal muscle attachments, and extreme buttressing of facial bone to absorb chewing stress). Claims that morphology is always the more valid taxonomic criterion were also invalid. Robinson finally criticized Tobias on the use of the LxB index again, stating that variation seen in the australopithecines can easily accommodate *Homo habilis*. Virtually no genus of early hominid could be sorted based on the dental shape, and since the taxon Tobias was defending was in a separate genus from *Australopithecus*, the trait must be able to separate out genera, which it could not (Robinson, 1966:959).

Others as well disputed the new taxon. Although arriving at a similar estimate of the cranial capacity of the Olduvai Bed I hominine, Holloway disagreed with Tobias on the taxonomic attribution of the specimen, claiming that "it would not be unlikely that on the basis of cranial capacity, at least, the 'pre-*Zinj'* materials are within the australopithecine taxon of early hominids (Holloway, 1965:206)." Montagu believed *Homo habilis* to be an early representative of *Homo erectus* (1964:918), while Oakley and

Campbell chastised the namers on the technical ground of violating some of the rules of the ICZN (1964:732). Campbell as well criticized the namers for violating the ICZN (1964:451). He also criticized Leakey for using taxonomic labels as mere conveniences, without accepting the biological reality of species.

A year after the new name was proposed, Tobias presented a synthesis of the status of the East African finds, and their bearing on human evolution. He felt that "in the great majority of measurable features, such as the size of the teeth, their shape indices, the cranial capacity, the dimensions and robusticity of the mandibles, and the curvature of the cranial bones, the remains of *Homo habilis* lie just at the extreme of, or outside, the range of variation of the australopithecines (Tobias, 1965:392)." *Homo habilis* was intermediate between *Australopithecus* on the one hand, and *Homo erectus* on the other. Tobias recognized that *Homo habilis* was a transitional form, but lamented that the current system of classification was incapable of dealing with morphological intermediacy (a common and all too real complaint of all paleontologists).

Within the Australopithecinae, Tobias recognized only one genus, *Australopithecus*, and he saw only *Homo* within the Homininae. He pointed out that should this bigeneric system be adopted, the need for two subfamilies (Australopithecinae and Homininae) would fall away (Tobias, 1965:394). It is from here that the vernacular term 'australopithecine' is derived, and it is for this reason, the loss of the validity of the term, that it has been used in this study to encompass all non-*Homo* early hominids known as a vernacular form only. Tobias also recognized that some preferred to retain *Paranthropus* (especially Robinson) and even *Pithecanthropus* (Le Gros Clark). However, he and his co-namers, Leakey and Napier, chose to accept only *Australopithecus* and *Homo*.

Commenting on Tobias' article, Day pointed out that taxonomy within the hominids had been bedeviled by excessive nominae, and that Linnean taxonomy was not designed to deal with intermediaries. However, he appeared to accept the new species, both on morphological and cultural grounds (i.e., the presence of tools) (Day, 1965:399).

Howell commented that he was convinced that 'Zinj' was at best specifically distinct from known forms of *Australopithecus*, but that the *Homo habilis* materials might belong within *Homo erectus* (or even *Homo modjokertensis*) rather than a new species (Howell, 1965:400). He concluded that Robinson had been correct, that the Bed I material was *Australopithecus*, and Bed II was *Homo erectus*.

Von Koenigsvald on the other hand, still accepted the existence of *Zinjanthropus*, *Pithecanthropus*, *Meganthropus*, and *Atlanthropus*, and he felt the new taxon was fully justified (von Koenigsvald, 1965:402).

Robinson again listed out his reasons for rejecting *Homo habilis*, adding that some of the actual traits used were of dubious validity, and that many of the measures made were very different for different researchers, allowing bias to enter (Robinson, 1965a:404). He also criticized Tobias for employing all australopithecines (including *Paranthropus*) in comparisons with *Homo habilis*, rather than just *Australopithecus*. Robinson never accepted *Paranthropus* as a junior synonym for *Australopithecus*, and thus felt two genera were being improperly combined to compare with one species of *Homo*.

Leakey as well joined the debate, supporting Tobias' view that *Homo habilis* was a valid taxon distinct from *Australopithecus*. Looking at the v-shape contour of the mandibles of various hominids, Leakey felt that, without doubt, *habilis* belonged in *Homo*, not *Australopithecus*. However, he disagreed completely with Tobias when it came to larger scale phylogenetic relationships. He felt that ". . . morphologically it is almost impossible to regard *Homo habilis* as representing a stage between *Australopithecus africanus* and *Homo erectus* (Leakey, 1966:1280)." Based on the location of the maximum cranial width, and on occipital morphology, Leakey found it impossible to place the two in an ancestor-descendent state. He felt instead that *Homo habilis* would quite likely be ancestral to *Homo sapiens*, but that both *Australopithecus* and *Homo erectus* were distinct side branches that both went extinct.

Robinson replied to this statement by pointing out that, since the original naming, the authors had split on more than just the last point of Leakey. Tobias had separated Bed I and Bed II remains from Olduvai, while Leakey had not. Therefore, when Leakey compared the mandibular profiles in the last mentioned article, he was comparing what both Robinson and Tobias considered to be *Homo erectus* (Robinson, 1967:77, note 2). Robinson felt this supported his position that the taxon *Homo habilis* was unnecessary and redundant.

Robinson went on with a discussion of the different levels of taxonomic inference, pointing out differences in meaning for both genus and species. He then applied these to the discussions that had been going on regarding the various characters used to define *Homo habilis* and again concluded that the dental and much of the cranial evidence was insufficient to distinguish *Homo habilis* from either *Homo erectus* or *Australopithecus africanus*. He followed this line of reasoning then to the conclusion that the distinction between *Homo* and *Australopithecus* was not zoologically valid, and that the two should be considered congeneric (Robinson, 1967:98). The nomen *Homo transvaalensis* would then have precedence for the fossils previously regarded as having been *Australopithecus africanus*, since *Homo africanus* had already been used in the literature by Broom for the Boskop finds. And, since there was no clear phylogenetic distinction between *Homo erectus* and *Homo sapiens*, the two would be combined with the nomen *Homo sapiens* taking precedence. *Paranthropus robustus* and perhaps *boisei* would remain distinct taxa. A side effect of this new system of hominid classification would be that the genus *Australopithecus* would disappear, and with it the subfamilies Australopithecinae and Homininae. Robinson even felt the vernacular term australopithecine should fall away as well.

Other new taxa were being named as well, though they provoked far less debate. A new taxon, *Tchadanthropus uxoris*, was named to accommodate fossils found at Yayo, in Chad (Coppens, 1965:2869). It was based on a severely weathered and quite undiagnostic cranial fragment, which Coppens admitted bore strong resemblences to *Australopithecus* (Coppens, 1965:2870). The new species never achieved the status accorded to the other finds being made at Olduvai, and was never widely accepted.

A short time later, new finds in the Omo Valley produced yet another hominid species, this time referred to as *Paraustralopithecus aethiopicus* (Arambourg and Coppens, 1967:590). This new taxon was based entirely on one edentulous mandible. It was recognized as an australopithecine, but the authors felt it to be specifically and generically distinct from any other known taxa. The fact that there were no teeth at all in the mandible made it very difficult to believe the new claim, and it was also never well received. This taxon, and its type specimen mandible, would make a comeback 20 years later, and form part of another new, ill-founded species, to be discussed below.

When discussing the status of the taxonomy of the fossil hominids, Buettner-Janusch chided anthropologists for not employing a proper understanding of the biological meaning of species. He felt that, when naming new species, "we must take account of the variability in the same anatomical systems of related living species and genera when making a diagnosis of a new taxon (Buettner-Janusch, 1966:158)." The different species names imply complete genetical isolation of the two populations in the past. When looking at phyletic lineages, he noted that different species named by anthropologists ". . . are separate species if the particular fossils represent successive populations in a single lineage, in which the evolutionary change between the different time stages is sufficiently great *so that the two populations differ to the same extent as do two species which live today* (Buettner-Janusch, 1966:173, italics mine)." Again, outgroup comparison was seen as an important and valid scientific methodology.

Buettner-Janusch was not convinced that *Homo habilis* was a valid species. He cited many other authorities who had noted that many of the traits used by Leakey et al. were not taxonomically valid. The *Homo habilis* finds were not identical to australopithecines morphologically, but "the differences are too small to justify the erection of a separate taxon (Buettner-Janusch, 1966:167)." He was also unwilling to accept *Zinjanthropus* as a valid taxon.

Rather than accept all the hominid species that had been named in the past, Buettner-Janusch advocated a severe reduction in their numbers. He proposed that the genus *Australopithecus* should be sunk into *Homo*, and all its fossil members be renamed *Homo africanus* (Buettner-Janusch, 1966:171). He also saw no valid reason why the species *Homo erectus* should not be considered a member of the species *Homo sapiens*. He allowed them a subspecific status, *H. s. erectus*, but insisted that if alive today, they would be fully inter fertile with modern humans (Buettner-Janusch, 1966:172).

Buettner-Janusch was somewhat less clear on the distinction between the 'robust' and 'gracile' species. He indicated that it was entirely possible that *Australopithecus robustus* could belong within the species *Homo africanus*, although it was also possible it could warrant a different taxon. He left the decision open at the time, providing no definition of the *Australopithecus robustus* group. He made no mention at all of the *Australopithecus boisei* group, and presumably did not consider it a valid taxon (as he also did not accept *Zinjanthropus*).

In 1967, Tobias published his landmark volume on the skull of '*Zinjanthropus*', OH5. In his discussion of the taxonomic history of the australopithecines, Tobias reached the same conclusion that has been discussed in this present study; namely, that a splitting trend occurs in the early stages in the discoveries of a group of fossils but that, as time goes by, a lumping trend occurs as more fossils accumulate and ranges of variation are better understood. I differ from this view in believing that splitting trends occur not just in the early stages of discovery, but also in light of large infusions of new fossil material into the record. These new infusions often lead to new taxa, though further analysis tends, not so much to validate these taxa, as to extend the known ranges of variation of fossil groups. Again, the inadequacy of Linnean taxonomy for dealing with intermediary fossil stages further fuels this discrepancy, and is primarily responsible for the confusion that accompanies and produces taxonomic overabundance.

Tobias felt in 1967 that the time was right for a major reconsideration of the Hominidae, as numerous fossil finds from both South Africa and other areas in east Africa had produced a wealth of new information in the immediately previous years. He felt that the new abundance of fossils provided a body of evidence that irresistibly pointed toward all australopithecines belonging to one single genus, *Australopithecus* (Tobias, 1967b:219).

In this work, Tobias also made mention of the concept of 'phyletic valence'. He was of the opinion that it makes little difference if a trait is or is not capable of separating out two outgroup taxa. The only important factor is whether or not a trait can separate out the taxa being directly studied. More simply stated, it does not matter whether cranial capacity, or the development of the supra-orbital torus, can or cannot separate out two species of chimpanzee; the only important point is whether or not these traits can separate out the species of *Australopithecus*. If one accepts this criticism as valid, then it can be used to demolish the entire argument upon which this thesis is based at its theoretical foundation. However, not all have agreed with this argument, and neither does this author.

To accept this point of view is to accept that virtually any distinction, regardless of its triviality, is capable of separating out species, and that no measuring stick can ever be effectively devised to account for interspecific variation. The problems inherent in this argument are manifested, by way of example, in the work of Rak (1983). Although a work of great insight and anatomical detail, the amount of taxonomic significance that has been attached to *The Australopithecine Face*, and to the numerous facial morphological minutiae it describes, far exceeds the facts presented. It must be tested whether or not such morphological facial minutiae are in fact capable of separating out other taxa, and the only way to do this is through outgroup comparison.

The words of Simons and Pilbeam must be reiterated here that, "in order to establish a valid species it should be necessary to show characters in the available fossil material which purport to be of the same magnitude as those which separate related living species (Simons and Pilbeam, 1965:101)." Simons went on to claim that the "'morphological space' between time successive species and genera [should be] about the same as that which separates related living species and genera (Simons, 1967:315)." Brace as well made commentary relevant to this topic when discussing the taxonomic overabundance that existed in the early days of human paleontology, and which lead to the creation of at least 8 genera and 12 species of early hominids. He felt that "minute details of morphological difference were taken to justify the [numerous] taxonomic designations, and only very much later was there any concern expressed for *whether such features were of taxonomic relevance in distinguishing taxa of living primates* (Brace, 1973:202; italics mine)." Finally, Le Gros Clark as well felt that "paleoanthropologists . . . should agree to refrain from creating any new species or genus on the basis of a fossil specimen unless it can be demonstrated with reasonable assurance that the skeletal and dental characters of the specimen deviate from those already known *to an extent at least equivalent to the differences between recognized species or genera in recent representatives of the same or allied groups* (1955:16; italics mine)." It is firmly held in this thesis that, in order for a trait to be considered taxonomically valid for one fossil species, it *must* be able to statistically separate out other closely related taxa.

Tobias went on to discuss the taxonomic debate that surrounded OH5 after its discovery and naming as *Zinjanthropus boisei*. He noted that Robinson had immediately called the new genus biologically unmeaningful, reattributing it to the genus *Paranthropus*. Others too, as noted above, considered the new taxon to be invalid. Tobias then noted that he, Leakey and Napier had subsequently formally recognized only one genus, and 'Zinj' had been added to the hypodigm of *Australopithecus* without affecting the formal diagnosis given the genus by Le Gros Clark in 1964.

The distinction between *Australopithecus* and *Paranthropus* was contested, and it was concluded that the differences noted by Robinson between the anterior, as well as the posterior, dentition were not significant enough to warrant Robinson's claims of significant ecological differences between the two (Tobias, 1967b:228). The distinct diets that Robinson felt existed, were to Tobias, artifacts of small sample sizes and incorrect interpretations. As well, the other morphological differences stated as being important for separating *Paranthropus* from *Australopithecus* were shown to be, for the most part, strongly related to differences in the size of the teeth and mastication musculature; they were artifacts of size differences, not generic distinctions.

Regarding his earlier stance (Leakey, Tobias and Napier, 1964), Tobias felt the evidence had become strong enough to warrant the sinking of the sub-genera they had proposed in 1964. *Australopithecus* would be the only genus, containing *Australopithecus africanus* and *Australopithecus robustus* (Tobias, 1967b:231). He further removed the sub-generic distinction of *Zinjanthropus*, and named one only species in east Africa, *Australopithecus boisei*. He described his reasons for maintaining the specific distinction between *boisei* and *robustus*, stating that ". . . the Olduvai australopithecine differs from *A. robustus* in a similar manner to that in which the latter differs from *A. africanus* (Tobias, 1967b:233)." He completed the volume by formally defining the genus *Australopithecus*, and its constituent species, and discussing the phylogenetic status of the australopithecines (with the formal sinking of all other genera, the sub-family Australopithecinae fell away, although the vernacular term 'australopithecine' is still used today).

The importance of using a proper understanding of taxonomy amongst paleoanthropologists was strongly propounded by Simons in 1967. He criticized many researchers of the day for inventing numerous new taxa which had no biological reality. He never accepted *Zinjanthropus* as a valid genus, and in fact stated that, based on the known samples of 'robust' australopithecines, there was not much evidence that *Australopithecus robustus* and *Australopithecus boisei* were even separate species (Simons, 1967:308). Neither did he accept the distinct status of the taxon *Homo habilis* as separate from *Australopithecus africanus* (Olduvai Bed I materials) or *Homo erectus* (Olduvai Bed II materials). He relied heavily upon Robinson for his argument, but split sharply with him on the point of the distinction between *Australopithecus* and *Homo*. Whereas Robinson would place both in the same genus, Simons felt there was ample evidence to separate them (Simons, 1967:312). He also differed with Robinson in not wishing to place *Australopithecus* and *Paranthropus* into separate genera, claiming that "the dental and cranial anatomy of *Australopithecus africanus* and *A. robustus* do not, in fact, provide grounds for separating them at the generic level (Simons, 1967:314)." Finally, while discussing *Tchadanthropus uxoris*, Simons claimed that "it is preposterous to indicate, by giving it a Linnean binomen, that it represents a population distinct on both the specific and generic level from any other hominid population (Simons, 1967:330)." He clearly felt that taxonomic overabundance was a significant problem within the field of paleoanthropology.

While later discussing the taxonomic position of the newly named taxon *Paraustralopithecus aethiopicus*, Simons stated quite clearly that "this mandible certainly cannot be shown to represent a new species because of its incompleteness. It should never have been given a taxonomic designation (Simons, 1969:21)." The entire genus and species had been named on a single edentulous mandible, a remarkable taxonomic feat. In spite of the absurdity of the new taxon, and in spite of its subsequent dismissal, it made a reappearance in 1986 under the guise of *Australopithecus aethiopicus*, a similar taxonomic feat to be discussed below. Equally strongly, Simons noted that "it will not be possible for scholars in this field to devote their principle energies to the recovery of new scientific data as long as their attention is drawn away into the refutation of weakly founded names and the insubstantial deductions which surround their formulation (Simons, 1969:22)." This statement will be particularly resounding when we begin to discuss the current resurgence in taxonomic overburdening of the fossil record below.

In 1967 F. Clark Howell provided an excellent summary of recent advances in human evolutionary studies. His opinion was that the time had come for a reappraisal of the taxonomic status of the Hominidae, both since much confusion was still evident in the field, and since the fossil record had been greatly expanded in the previous few years. He agreed with Leakey et al. that only one genus should be recognized within the australopithecines, that being *Australopithecus*, and that said genus should contain two subgenera, *Australopithecus* and *Paranthropus* (Howell, 1967a:474). Conspicuous by absence was *Zinjanthropus*, which he presumably discounted entirely.

When considering *Homo habilis*, Howell noted that, although the mandibular and dental evidence was insufficient, the vault form and cranial capacity of the fossils "suggest[ed] a new taxon. . . [and] the designation of *Homo habilis* as a new taxon may indeed prove warranted (Howell, 1967a:479)." He further believed that what was referred to as *Meganthropus palaeojavanicus* in Java was in reality *Homo habilis*, not *Paranthropus* as Robinson had claimed. He also indicated in his revised classification of Hominidae that he felt *Homo habilis*, *Homo erectus* and *Homo sapiens* were evolutionary species. In effect, he believed that they formed a continuous phylogenetic lineage, and that artificial boundaries had been erected as aids to classification, rather than real cladogenetic events (see Simpson, chapter 1, section 1.2.4, this study, for discussion of evolutionary species).

In 1968, Robinson published another version of his landmark paper, *The Origin and Adaptive Radiation of the Australopithecines*. It was originally presented in 1961, and a subsequent edition of the book it appeared in was put out in 1968. The 1961 version was not available to this author, but it appears as though it was republished in 1968 unaltered, although accompanied with an addendum which incorporated new finds and taxa into the analysis. The previous was important to note, as it was in this paper that Robinson officially diagnosed what he considered to be all of the valid hominid genera, prior to *Homo habilis*. The definitions used by Robinson will be thus incorporated into this analysis from the 1968 version, and a discussion (though no analysis) of the 'latest' finds (i.e. *Homo habilis*) will be given below.

Robinson was again adamant that two early hominid genera were present in South Africa, *Australopithecus* and *Paranthropus*. He outlined many morphological characteristics which separated the two genera, and gave formal diagnoses to each, as well as to the genus *Homo*. He also again reasserted that *Meganthropus* as a genus was invalid, and should rather be considered a member of the genus *Paranthropus*. *Zinjanthropus* of Leakey was considered invalid, although the specific status of *boisei* was transferred to *Paranthropus* unaltered.

In the accompanying addendum Robinson again pointed out that the new taxon *Homo habilis* was invalid, both on taxonomic and morphological grounds (Robinson, 1968:170). The naming of the species appeared to violate the International Code (ICZN). Also, the materials referred to *Homo habilis* appeared to represent more than one taxon; Robinson claimed that the Bed I fossils were actually *Australopithecus*, while the Bed II remains were in fact *Homo erectus*. He pointed out the fact that it might be that Olduvai was revealing the evolution of *Australopithecus* into *Homo erectus*, and that transitional stages had been found (Robinson, 1968:172). As a final note Robinson stated that "it seems to me that *Australopithecus* represents merely the earlier stages of the establishment of the adaptive pattern characteristic of *Homo* and therefore does not merit generic distinction . . . (Robinson, 1968:173)." He felt there was no meaningful generic distinction between *Homo* and *Australopithecus*, since they were essentially a direct phyletic lineage.

Following his great monograph on the 'Zinj' skull, Tobias undertook again to assert his rediagnoses of the different australopithecine species. As Tobias recognized only two hominid genera, he felt that the need for subfamilial status within the family Hominidae fell away, though the vernacular terms would still be quite useful (Tobias, 1968:282). He also dropped the subgeneric status of *Australopithecus*, *Paranthropus*, and *Zinjanthropus*. He also reiterated that *Australopithecus boisei* was as distinct from *Australopithecus robustus* as the latter was from *Australopithecus africanus* (Tobias, 1968:293). He then again redefined the genus *Australopithecus*, as well as each of the species he believed valid.

The important addition in this article was a discussion of the taxonomy of *Homo*. The taxon *Tchadanthropus uxoris* had recently been named by Coppens as a new genus and species. Tobias, however, considered it to be *Homo erectus*, a stance Coppens had apparently come to share (Tobias, 1968:296). As for *Telanthropus capensis*, Tobias stated that since Dart felt it to be an australopithecine, while Robinson sank it into *Homo erectus*, serious consideration had to be given to his argument that it was actually an intermediate form, one he had named *Homo habilis* a few years earlier. *Homo habilis* bridged the gap between the genera *Homo* and *Australopithecus*.

It was around this time too that Tobias first proposed his taxonomic scheme employing bigeneric and bispecific nomina to represent intermediate fossil forms. He bemoaned the fact that classical Linnean taxonomy was entirely unable to deal with intermediary fossil forms (Tobias, 1967a:46). The position of *Homo habilis* as intermediate between *Australopithecus* and *Homo erectus* was fully recognized by Tobias, and it was to accommodate this 'missing link' that he devised his new scheme. It was at this point too, that the possibility of evolutionary side-branches in the genus *Homo* was raised by Tobias, who asked "dare we admit of side-branches, of a cladistic element, in the Pleistocene phylogeny of modern man? (Tobias, 1967a:46)."

He later elaborated on this scheme, and also outlined what was to become the 'classic' phylogenetic tree of the hominids:

A. robustus/boisei   Homo
V
|
A. africanus

Tobias saw a very *africanus*-like animal representing the basal hominid stock, if we were to regress through time to the point of departure from the apes (Tobias, 1968:307).

A brief return was made to the subject of *Telanthropus* in 1968 by Milford Wolpoff. He believed that "no morphological evidence validly distinguishes the [*Telanthropus*] specimens from the other australopithecines (Wolpoff, 1968:477)." He was especially referring to the *Paranthropus* remains found alongside the *Telanthropus* material at Swartkrans. Wolpoff maintained that there was only one species of *Australopithecus*, and that the claim of *Homo habilis* had been "effectively demolished" (Wolpoff, 1968:478). *Australopithecus* evolved directly into *Homo erectus*, and the claim that an aberrant side branch of robust australopithecines ever existed was false. They fell within his proposed estimated population range for *Australopithecus*. Although he did not accept *Telanthropus* as a valid taxon, Wolpoff used it and its similarity to the *Paranthropus* remains found at the same site as proof of his claim of the single species hypothesis.

Of significance in Wolpoff's work was his claim that "one way to determine the taxonomic relevance of a trait is to compare its observed variation within a *known* species to its variation *between* known or postulated species (Wolpoff, 1968:487; italics in original)." He felt that paleoanthropologists ". . . surely do not wish to base our taxonomic determinations on criteria that cannot be used to distinguish *Homo sapiens* from the larger australopithecines (Wolpoff, 1968:490)." Using outgroup comparisons, Wolpoff felt justified in including all australopithecine material into a single species. However, there were a number of problems with Wolpoff's analysis.

In a reply to Wolpoff's assertions, Gutgesell stated that her analysis of the same material was "inconsistent with Wolpoff's conclusions and the single species hypothesis of human evolution (Gutgesell, 1970:565)." She first demonstrated that Wolpoff's stratigraphic interpretations were wrong, and that, in fact, there were two distinct forms of hominid living sympatrically at Swartkrans. She then discussed a large amount of morphological evidence which Wolpoff considered to be of little importance, though Gutgesell proclaimed its taxonomic value; "thus it is clear that *Paranthropus* and "*Telanthropus*" differ considerably in non-dental cranial and mandibular morphology . . . [and] these differences are significant (Gutgesell, 1970:569)." She further criticized Wolpoff for using an improper statistical technique to attempt to separate the two samples from Swartkrans. Instead, she re-examined his material using the Student's t-test, which is the precise test that this thesis will employ. Gutgesell concluded that Wolpoff's interpretations were wrong, and that there were two distinct forms of hominds living sympatrically, thus also disproving the single species hypothesis as well.

Discussing other problems in the taxonomy of fossil hominids, particularly the distinction between *Australopithecus robustus* and *Australopithecus boisei*, McKern and McKern were inclined to believe that the two represented only one taxon, *Australopithecus robustus*, a sister group to *Australopithecus africanus* (McKern and McKern, 1969:80). However, when it came to *Homo habilis* and *Telanthropus capensis*, the authors chose to wait until further study had been completed before making a decision as to the validity of these taxa. This in spite of the fact that one of the original namers of *Telanthropus capensis* had recanted this name, and that no one at the time really considered *Telanthropus* a legitimate nomen anymore.

Again, others still refused to accept *Australopithecus boisei* as a valid species, allowing only *Australopithecus robustus* and *Australopithecus africanus* into the australopithecine family (Pfeiffer, 1969: 67).

The year 1967 marked the beginning of the tremendous proliferation of the hominid fossil sample from east Africa. An international expedition of French, Kenyan and American paleontologists discovered large quantities of hominid fossils in the

Lower Omo Basin in Ethiopia (Howell, 1968). Reporting on the earliest of these finds, Howell indicated that all the fossils found fit well within the known australopithecine taxa of South Africa and Olduvai (Howell, 1969). Two of the mandibles found were identified as 'robust' specimens and attributed to *Australopithecus boisei*, due to the extreme large size. The remains found in all the other localities were considered to be closest to *Australopithecus africanus*, although these attributions were tentative pending further finds in the area. These finds were of extreme importance because they allowed for the first precise dates of 'gracile' australopithecines. They also extended the geographical range of the species by thousands of miles. As well, the accepted time frame for the australopithecines was pushed back, for the 'robusts' in particular, over 500,000 years (Howell, 1969:1239).

In a discussion of the estimated cranial capacity of the Olduvai Hominid 7, Wolpoff had indicated that he was unable to accept the existence of the taxon *Homo habilis*, since this value fell within accepted standard deviation of the species *Homo africanus* (Wolpoff, 1968:182). From this it can be deduced that Wolpoff supported Robinson in his reassessment of the systematics of the australopithecines. Pilbeam criticized Wolpoff for using an improper statistical technique, and recommended that the Student's t-test be used (Pilbeam, 1969:386). Oddly, Pilbeam further commented that until the statistical calculations were more secure, taxonomic conclusions should not be drawn about *Homo habilis*, despite the fact that he himself had previously done so (Pilbeam and Simons, 1965). Wolpoff replied that his statistical procedures were correct, and that

Homo habilis could not be separated from *Homo africanus* based on its cranial capacity (Wolpoff, 1970:747). Pilbeam responded by stating that population variability must be taken account of, and that the OH7 material did in fact appear to be significantly different from *Australopithecus africanus* material, concluding that "it would seem most reasonable, therefore, not to include hominid 7 in *A. africanus*, but to refer it to another species of the genus *Australopithecus* (Pilbeam, 1970a:748)."

Pilbeam had recanted an earlier claim made about the status of *Homo habilis*, and particularly OH7. In the previous year, in an article he cited in the above 1970(a) work as proof of his claims of the difference of OH7, he stated ". . . the present evidence favors placement of the Bed I "*Homo habilis*" material in the genus *Australopithecus* and possibly in species *A. africanus* as well (Simons, Pilbeam and Ettel, 1969:259)." He, along with his co-authors, felt in 1969 that it had yet to be convincingly demonstrated that "the type mandible (OH 7) and other material from Bed I (OH 8) samples a population which is specifically distinct from South African *Australopithecus africanus* populations (Simons, Pilbeam and Ettel, 1969:259)." He apparently changed his mind about the value of OH7, and it was as a result of this that he felt OH7 should be excluded from *Australopithecus africanus*.

In his discussion of the overall taxonomy of the early hominids, Pilbeam stated that he accepted only one genus, *Australopithecus*, though this was only tentatively (Pilbeam, 1970b). He also believed that the *Telanthropus capensis* remains were actually members of the genus *Australopithecus*, but was uncertain as to their specific status, be it *Australopithecus africanus* or *Australopithecus capensis* (Pilbeam, 1970b:144). Oddly, Pilbeam provisionally classified the Olduvai Hominid 5 skull as *Paranthropus boisei*, although he recognized only *Australopithecus* as a valid genus; and, immediately after his attribution, he referred to the species as *A. boisei* (Pilbeam, 1970b:157). It would appear that he did in fact intend for the species to be designated *Australopithecus boisei*. As regarded *Homo habilis*, Pilbeam indicated that he saw it as an invalid species. Instead, he felt it to be conspecific with *Australopithecus africanus*, with only a subspecific designation (Pilbeam, 1970b:162).

The first reports of hominid remains from Koobi Fora, near Lake Rudolf in Kenya were made by Richard Leakey in 1970. Five hominid fossils had been recovered, including a rather complete skull which bore strong resemblences to *Australopithecus boisei* (Leakey, 1970:223). Another fragmentary cranium was found, but its morphology was different from the other, bearing resemblences to either a 'gracile' australopithecine, or else an early member of the genus *Homo* (Leakey, 1970:224). A date of 2.61 ± 0.26Myr was attached to the finds, although caution was expressed that some contamination may have occurred (Fitch and Miller, 1970:228). This date was obtained using the then new ^{40}Ar/^{39}Ar technique.

In the *Atlas of Fossil Man*, Brace et al. again outlined the single species hypothesis, claiming that size differences in the various australopithecine species were due to the use of only a few well preserved, but quite divergent, examples to represent entire species (Brace, et al. 1971:20). They allowed for only one species, *Australopithecus africanus*, and included within it all forms previously referred to as *Paranthropus*, *Plesianthropus*, *Telanthropus*, *Tchadanthropus*, *Zinjanthropus*, possibly *Meganthropus*, and perhaps others (Brace, et al. 1971:20). Brace et al. also apparently only accepted two species within the genus *Homo*, *Homo erectus* and *Homo sapiens*, conspicuously omitting *Homo habilis* from their taxonomy.

In 1971 another fossilized hominid skull was found at Olduvai, and designated OH24 (Leakey et al., 1971). This skull was considered to be a representative of *Homo habilis*. There were certain questions that arose regarding some of the morphological features of the new skull, however. Morphologically, it resembled the material from Bed II at Olduvai, which both Robinson and Tobias had called *Homo erectus*. Chronologically, the skull was thought to be nearer to the Bed I *Homo habilis* materials. As such, Leakey et al. questioned the attribution of the Bed II materials to *Homo erectus*, claiming they were now morphologically much more similar to Bed I, based on the new skull find. As an explanation, they relied upon sexual dimorphism to account for the differences between the new skull and *Homo habilis*, although they did not rule out the possibility of a taxonomic difference (Leakey et al., 1971:312). The attribution of OH24 to *Homo habilis* was therefore tentative.

An anonymous reviewer discussing the new skull bemoaned the fact that many of the features of this "clearly *Homo*" skull, in fact, did not meet the criteria set out in 1964 when Leakey et al. redefined the genus *Homo*. Its cranial capacity fell short of their "rubicon", and the extreme dishing of the face of the new skull also argued against it belonging in the genus *Homo*. The reviewer felt that "the differences in certain features in *Australopithecus africanus* and *Homo "habilis"*. . . are probably due only to normal variation within a single species (Anonymous, 1971: 295)." Criticizing the actual rediagnosis of the genus *Homo*, the reviewer claimed that, "the revised definition of the genus *Homo* included several cranial features that differed only slightly from, or overlapped with, those found in *Australopithecus*. Indeed, many of the cranial criteria were so ambiguously flexible that perhaps only the odd gorilla would have been denied membership (Anonymous, 1971:294)."

The factor of sexual dimorphism, until this time, had played an insignificant role in the study of early hominids. Brace undertook to correct this oversight, and reached the conclusion that the differences in morphology between the various australopithecine sites might actually be a result of sexual dimorphism (Brace, 1972:33). He was not suggesting that only males were being found at Swartkrans, and females at Sterkfontein. Rather, he was pointing out that type specimens of each locality might be influencing the overall perception of the differences between the sites. The extremely large male SK48 and the much smaller female STS5 were used to characterize the sites of Swartkrans and Sterkfontein respectively, and may have colored the perceptions of the two. Brace believed that the amount of sexual dimorphism in the human lineage was much greater in the past, and that modern comparisons relied too heavily upon the amount of dimorphism that characterizes modern humans, thereby underestimating australopithecine sexual dimorphism. He did not believe that there was a legitimate taxonomic distinction between *Australopithecus africanus* and *Australopithecus/*

Paranthropus robustus (Brace, 1972:36). Instead, the differences seen between the two were simply due to sexual dimorphism.

Brace et al. followed this up by turning their attention to the newly proposed taxon, *Homo habilis.* They concluded that, based on graphical and statistical analysis, the type specimen of *Homo habilis*, OH7, could not be distinguished from *Australopithecus africanus*. As well, the paratype, OH13, could not be distinguished from *Homo erectus*, and neither could another group of *Homo habilis* fossils, collectively labelled OH16, be separated from *Australopithecus africanus* (Brace et al., 1972:66). They thus suggested that, since *Homo habilis* was an empty taxon, it should formally be sunk.

The taxonomic position of *Homo habilis* was unclear even to those who supported its existence. Pilbeam and Zwell were unsure whether to refer to it as *Homo habilis* or *Australopithecus habilis* (Pilbeam and Zwell, 1972:69). In their study of the morphological variation of the dentition of the australopithecines, they noted that the period between 1.5 and 2.0 million years ago, there were almost certainly two hominid lineages evolving coevally in Africa. One, *Homo* (or *Australopithecus*) *habilis*, evolved into *Homo erectus*, while the other, which included both *Australopithecus robustus* and *Australopithecus boisei*, became extinct (Pilbeam and Zwell, 1972:78). They clearly recognized the 'robust' lineage as possessing two distinct species, though no details were given as to why.

Pilbeam later clarified his position somewhat by stating that "I believe that the present evidence favors its [*Homo habilis*] description as a species of *Australopithecus*, *A. habilis* (Pilbeam, 1972:129)." He felt that, owing to the similarities in brain volume, other cranial features, dental and mandibular characteristics, and postcranial anatomy between *Homo habilis* and *Australopithecus africanus*, the taxon should be housed within *Australopithecus* rather than *Homo*. He also accepted the Tobias (1967) version of the taxonomic status of the genus *Australopithecus*, rejecting Robinson's use of *Paranthropus*. He also accepted Tobias' attribution of *boisei* to *Australopithecus* as a valid species, possibly as a descendent of *Australopithecus robustus*.

The existence of at least two lineages in Africa during the Pleistocene was confirmed by Richard Leakey based on his research in Kenya. Most of the specimens recovered belonged to the genus *Australopithecus*, though there were some that held strong affinities with *Homo*. One of the initial points Leakey made was that he believed the genus *Paraustralopithecus* to be invalid; it was simply a member of the genus *Australopithecus* (Leakey, 1971:241). He also indicated that the 'gracile' form of australopithecines being recovered at East Rudolf might actually be female versions of the more robust specimens, and that the robust australopithecines in general were a specialized side branch which made little evolutionary advance in the Pleistocene (Leakey, 1971:244).

In two succeeding articles in the *American Journal of Physical Anthropology*, Leakey et al. gave some careful, though admittedly not complete, descriptions of the fossils that were being found at East Rudolf (1971; 1972). The point of these papers was to put on record detailed but not exhaustive descriptions of the fossils so that other researchers could perform analyses of their own (as the authors realized they would do anyway). No detailed comparisons were performed, and the taxonomic designations of the materials was consciously avoided. The only claim made was that they were australopithecine fossils, although the authors again reserved the right to re-attribute any fossil they wished.

Although the initial reports were not comprehensive analyses, they did allow for some taxonomic conclusions to be reached. In following articles presented in *Nature*, Leakey indicated that he had found fossils he felt were representative of the genus *Australopithecus* as well as *Homo* (Leakey, 1971:244; 1972:265). He declined to officially attribute the fossils to any particular species, but he did speculate as to their affinities. The more 'robust' *Australopithecus* fossils were, to Leakey, quite similar to the Olduvai and Omo materials, and the implication was that he felt them to represent *Australopithecus boisei*. The more 'gracile' fossils were similar to the fossils of South Africa referred to as *Australopithecus africanus*. Rather than attribute them as such, however, Leakey referred them to the genus *Homo*, stating that "I believe that the *A. africanus* collection includes specimens that represent two separate lineages - *Australopithecus* and *Homo* - and the new evidence from East Rudolf illustrates the importance of re-examination of the earlier collections which serve as the basis for much of the current thought and teaching on human evolution (Leakey, 1972:268)." Unfortunately, he gave no indication as to why he believed the case to be true. Essentially, he felt that at least a portion of the *Australopithecus africanus* materials in South Africa would be better accommodated within the genus *Homo*.

Robinson replied to this article, claiming that the two were in essential agreement (1972a:240). He interpreted Leakey's comments as indicating that Leakey felt that the 'gracile' and 'robust' forms should be separated at the generic level. Since Leakey placed many of the 'gracile' South African forms in the genus *Homo*, just as Robinson had done, Robinson believed that "what Richard Leakey is doing with the East Rudolf specimens is biologically the same as I did with the South African material (Robinson, 1972a:240)." Robinson was of the opinion that "the differences between the South African and East Rudolf robust forms are small, as are those between the gracile samples, but the differences between gracile and robust forms in either region are much greater (Robinson, 1972a:240)." Leakey was apparently in agreement with this assessment, as he had noted similarities between his East Rudolf specimens of *Australopithecus* (which Robinson pointed out were equivalent to his *Paranthropus*, as Leakey excluded the 'gracile' forms from this consideration) and those from Olduvai. At the same time Leakey noted similarities between his 'gracile' forms and South African *Australopithecus africanus* materials, but he attributed his fossils to the genus *Homo*, and recommended the same for the South African ones.

That same year Robinson published his seminal work on hominid post-cranial anatomy, *Early Hominid Posture and Locomotion* (1972b). In this work he again outlined his taxonomic division of the early hominids into *Paranthropus* for the more 'robust' versions, and *Homo africanus* for the more 'gracile'. In a lengthy discussion of the rule of priority (ICZN), Robinson noted that the trivial name *africanus* had already been occupied in the genus *Homo*, and therefore the next most senior synonym, *transvaalensis,* should be for the designation of the former *Australopithecus africanus* materials. Again, however, Robinson noted that technically, *africanus* never conformed to the rules of the code (ICZN), and therefore had been invalidly used within the genus *Homo*. Therefore, since *africanus* had priority by virtue of Dart's usage of it in 1925, it should be the official nomen of the *Australopithecus africanus* materials within the genus *Homo*, thereby creating the taxon *Homo africanus*.

Based on his analysis of the post-cranial evidence of *Homo africanus* Robinson concluded that it had the same body proportions as modern humans, as well as being just as well adapted for bipedal locomotion (Robinson, 1972b:245). It was an omnivorous, dry plains dweller, skilled at tool use, and perhaps even tool manufacture. Robinson felt that "the adaptive pattern seems to have been in principle the same as that of man. Indeed, it seems to me that this *is* man, anatomically, ecologically, and behaviorally; for which reason I originally proposed that the generic name "*Australopithecus*" (sensu stricto) be sunk into *Homo* (Robinson, 1972b:246)." He still felt that *Australopithecus*, now *Homo africanus*, had descended from an ancestral *Paranthropus* population, which had itself come from an ancestral *Gigantopithecus* population (most likely *Gigantopithecus bilaspurensis*). At some stage, however, a generic threshold had been crossed.

He used as further proof of the difference between *Paranthropus* and *Homo* the suggestion by Tobias that the species *habilis* might be best accommodated in a bigeneric system, with both *Australopithecus* and *Homo* as 'parents'. Robinson pointed out that *habilis* did not indicate a need for a new system of taxonomy, but rather, indicated that the two genera were not validly distinct.

Robinson's analysis of the post-cranial remains also showed that *Paranthropus* was not of a similar adaptive plateau as *Homo*. It was less efficiently bipedal than *Homo*, was strictly herbivorous, and perhaps yet spent time in the trees (Robinson, 1972b:251). *Paranthropus* was probably not culture bearing, at least not in the sense of tool production or even use. And since there was no evidence that *Homo africanus* and *Homo erectus* were sympatric, Robinson concluded that they may have graded one into the other, while *Paranthropus* went extinct without issue. However, Robinson further stated that it was unlikely to expect that every deme of *Homo africanus* graded into *Homo erectus*, therefore it was more likely that one deme transformed into *Homo erectus*, and displaced the more primitive *Homo africanus* through competitive superiority (Robinson, 1972b:253).

Although Tobias' (1967) taxonomic scheme was gaining wide acceptance, not all believed it to be correct. Campbell (1972) attempted to re-evaluate hominid phylogeny, and came up with an entirely different scheme. Regarding *Homo habilis*, he believed that there was not enough room between *Homo erectus* and *Australopithecus africanus* to allow for its existence, and therefore demoted it to subspecific rank within *Australopithecus africanus* (Campbell, 1972:48). He reached a rather more difficult to understand conclusion when he discussed the distinction between

Australopithecus robustus and *Australopithecus boisei*. For *Australopithecus boisei*, he saw the evidence as being particularly strong that it was valid. However, he saw *Australopithecus robustus* as being an invalid taxon, and sank it to the level of subspecies within *Australopithecus africanus* (Campbell, 1972:48). He apparently saw no phylogenetic relationship at all between the two 'robust' species of *Australopithecus*. He saw *Homo habilis* and *Australopithecus robustus* in South Africa as being two subspecies of *Australopithecus africanus* (Campbell, 1972:45).

Campbell later elaborated on his scheme by stating that the chronological and morphological evidence showed that *Australopithecus boisei* was ". . . an independent lineage which separated from that leading to man sometime between 12 and 5 million years ago (Campbell, 1973:196)." It may have even been allopatric with *Gigantopithecus* in Asia! Should the scheme proposed, which saw *Australopithecus boisei* as a separate and ancient lineage, be accepted, it appeared that *Zinjanthropus* would be the accepted genus name. Campbell also claimed that certain East Asian fossils, namely those from Java, were actually a subspecies of *Australopithecus africanus*, referred to as *modjokertensis* (Campbell, 1973:197). He continued to classify all South African australopithecines as *Australopithecus africanus*, and refused the existence of *Homo habilis*.

In 1973 Richard Leakey announced the discovery of the partially complete cranium, designated KNM-ER1740. Although he was unwilling to attribute the skull to any specific taxon until further analysis had been undertaken, he did place it within the genus *Homo*

(Leakey, 1973a:450). He felt that the erection of a new genus for the find would be unnecessary. Since he indicated that the skull appeared significantly different from both *Australopithecus africanus* and *Homo erectus*, the implication was that he believed it most closely resembled *Homo habilis* from Olduvai. The dating of the skull was of extreme importance. The early estimates were around 2.61 ± 0.26 Myr, and if correct would indicate the presence of the genus *Homo* well before any previous estimate, contemporaneous with all but the oldest australopithecine materials (Leakey, 1973b:170). Leakey called for an extensive reassessment of the field of human evolution, as the existence of a large brained, fully bipedal member of the genus *Homo*, with associated tools as well, at 2.6 Myr threw the entire field into arrears (Leakey, 1973c:61). As will be seen below, however, the dating was not correct.

Many other finds were made in the East Rudolf area, and again Leakey was not willing to make specific attributions until a much larger sample, and hence a much better picture was available for study.

In late 1973, Tobias made the interesting suggestion that the Taung skull, the type specimen of the taxon *Australopithecus africanus*, might not in fact be an *Australopithecus africanus*. Recent new age estimates of the Taung site indicated that it was much younger than previously assumed, and that it might in fact be the youngest South African site, dated to around 1.0 Myr. Tobias thus suggested that the Taung skull might actually represent *Australopithecus robustus* (Tobias, 1973a:82).

In the same article, Tobias also tentatively attributed Leakey's ER1470 to *Homo habilis* (Tobias, 1973a:81). As well, he indicated that he considered *Australopithecus robustus* and *Australopithecus boisei* to represent a superspecies, a point which would incidentally, invalidate Campbell's view of the 'robust' species.

One ardent supporter of the single species hypothesis was Milford Wolpoff. He believed that the evidence for two hominid lineages in South Africa was unconvincing. Instead, he felt that the differences between the two types, the 'graciles' and the 'robusts', were the result of differences in body size (Wolpoff, 1973a: 137). Based on a reinterpretation of the differences between *Australopithecus* and *Paranthropus* noted by Robinson (1963; 1967; 1972), Wolpoff concluded that his "review of all available evidence provides no morphological or adaptive reason which would suggest more than one [taxon]. Under these circumstances, it seems best to consider the South African sample as representative of a single hominid lineage (Wolpoff, 1973a:137)." He was adamant that the differences were caused by sexual dimorphism (Wolpoff, 1973b:263).

Wolpoff (1971) also used the 'competetive exclusion' principle to argue against multiple lineages. His claim was that the primary adaptation of the hominids was culture, and as such, two different species with the same evolutionary adaptation would not be able to coexist as was claimed for the 'robust' and 'gracile' hominids (Wolpoff, 1971a:606). To support this idea, he showed that the summed post-canine tooth size of both the 'graciles' and the 'robusts' were inseparable, in spite of the differences the two lineages were hypothesized to have (Robinson, 1972). No difference in tooth size meant no difference in adaptation, which in turn meant no difference in species. Rather, the groups were seen as variants of a singular species, perhaps akin to subspecies (Wolpoff, 1971a:611).

Wolpoff was not alone in his belief in only one species of *Australopithecus*. Based on ecological arguments, Swedlund too accepted the existence of one species, apparently holding that the morphological variation between the different groups could be explained away by invoking polymorphism of the species (Swedlund, 1974:524).

Wolpoff later revised his view of hominid phylogeny, accepting the view of Mayr (1950). This was a direct result of his acceptance of the single species hypothesis (Wolpoff, 1971b:6). He felt that the differences between the 'gracile' and 'robust' hominids deserved no more than a specific separation, and was able to subsume them both within the genus *Homo*. The 'graciles' became *Homo africanus*, while the 'robusts' were called *Homo robustus* (Wolpoff, 1971b:128). This idea was not well met, and most authors rejected the inclusion of the australopithecines into *Homo*, for many of the same reasons as were mustered against Robinson. Further fossil discoveries would make this scheme quite untenable.

The early date applied to the ER1470 cranium caused a great deal of difficulty in the field of paleoanthropology. Its existence forced the split between *Homo* and *Australopithecus* back over a million years from its previous location (Tobias, 1973b:313). Altered perceptions of the dates of many of the hominid sites were causing a serious reappraisal of the field. Tobias again asserted his postulation that the Taung child might well belong to *Australopithecus robustus*, based on the revised dating of the Taung site itself (Tobias, 1973b:326). As well, the fossils of Makapansgat were being reassessed, and it was indicated by some that there were possibly two taxa represented there (Tobias, 1973b:319). Tobias felt these differences were the result of a speciation event occurring, and that here was found the split between the 'robusts' and the 'graciles'. A final point might be raised that Tobias again made mention of the superspecies *Australopithecus robustus/boisei*, although he did not explain precisely what he was implying by it. Presumably, he meant that the two were phylogenetically quite close, and perhaps were undergoing, or had just undergone, a speciation event.

All of these reassessments were taking place at a time when extensive new fossil finds were being made in East Africa, as well as in South Africa. A new excitement was being breathed into the field, and researchers were taking a much closer second look at their preconceived ideas. New 'heresies' were being introduced, and the orthodoxy was being challenged. Soon, the taxonomic situation in the field would be turned over again. It is precisely these periods of large influxes of new fossils that cause the critical self evaluations, as well as the recognition of new taxa. A resurgence of popular and scientific interest was then, and is now, provoking a proliferation of sites, fossils, and new hominid taxa. The light of sober reasoning will shine through soon, though, to again take a closer second look at the expanded fossil record, and place the field in its proper perspective.

Richard Leakey again reported on his ongoing work at East Rudolf in 1974. Although he again refused to officially attribute his finds to any particular species, he did speculate as to possible relationships. The specimens he had previously referred to as *Australopithecus* were claimed to be likely of the species *Australopithecus boisei*, although they did show similarities with *Australopithecus robustus* (Leakey, 1974:655). He also noted "striking similarities" between some of his fossil mandibles and those attributed to *Homo habilis*. One of the new skulls that had been found, ER1813, appeared to Leakey to be of a totally different type than he had seen before, and caused him to proclaim that "the possibility of more than two contemporary hominid lineages in the Plio-Pleistocene of East Africa may now have to be recognized, whereas previously one, or at most, two forms were assumed (Leakey, 1974:655)." As a result, he suggested that the genus *Australopithecus* be utilized to house the 'robust' species, *robustus* and *boisei*. A new (not named) genus should be erected to accommodate what were then called *Australopithecus africanus*, including the new ER1813, as well as OH24 from Olduvai. And finally, *Homo* should be used to house such fossils as ER1470, ER1590, as well as OH7 and OH16 from Olduvai (the type and paratype of *Homo habilis*) (Leakey, 1974:655-656). The reasons behind such a drastic taxonomic revision were not made clear.

Another diagnosis of the genus *Australopithecus* was provided in 1975 by Wolpoff and Lovejoy, this one taking into account recent new fossil finds as well as new analyses of the functional morphology of the fossils. The newly enlarged hominid sample almost required the revision, as the levels of acceptable variability of the species had been altered, quite drastically in some cases. Wolpoff and Lovejoy retained the generic distinction between *Australopithecus* and *Homo* because they felt that *Homo* was a much more variable genus, and future finds of even earlier australopithecines would raise the levels of variability for *Australopithecus* to a similar plateau (Wolpoff and Lovejoy, 1975:276).

A completely opposite point of view of human evolution was presented based on multivariate statistical analyses of the post-cranial skeletal remains of the australopithecines. Charles Oxnard claimed that the australopithecines had no place whatsoever in human phylogeny, and that "the genus *Homo* may, in fact, be so ancient as to parallel entirely the genus *Australopithecus* thus denying the latter a direct place in the human lineage (Oxnard, 1975:389)." He based this conclusion on a number of points, the main one being that, when the post-cranial remains were analyzed, they indicated that the australopithecines were much closer to the ape stage than to human. The net effect was that a far greater amount of climbing and perhaps even quadrupedal behavior was postulated for the australopithecines. Another of the points that convinced Oxnard was the assumption that the dating of the East Rudolf finds was correct, and that a *Homo* like creature lived contemporaneously with *Australopithecus* for perhaps a million or more years. However, as will be seen below, the East Rudolf sediments were not as old as thought, and the coexistence of the two genera was not as long term as was thought.

As a side point it can be indicated that Oxnard apparently was also unwilling to accept the existence of the taxa *Homo habilis* or *Homo africanus*. Rather, he only clearly indicated acceptance of *Australopithecus africanus* and *Australopithecus robustus*.

The methodology known as cladistics began to make an appearance in the field of paleoanthropology in the mid 1970's. Cladistics is a method of estimating phylogenetic relationships among fossil groups based on the presence of shared derived morphological features. Arising from such phylogenetic interpretations are cladogenic, or speciation, events, and as such this method can be used to determine taxonomic affinities of both entire taxa as well as individual fossils. This makes it a very important tool in the science of paleontology.

One of the first such analyses to be carried out was done by Eldredge and Tattersall in 1975. Based on cranial features, they were able to recognize three australopithecine species, *Australopithecus africanus*, *Australopithecus boisei*, and *Australopithecus robustus*. They did note, however, that the distinction between the 'robust' species was highly debatable. Notably absent in their phylogeny also was *Homo habilis*. They preferred to group the lower Bed I fossils of Olduvai (which were referred to as *Australopithecus habilis*) in with *Australopithecus africanus*. It was remarked that the relationships of *Australopithecus africanus* were expressed almost exclusively in primitive traits (Eldredge and Tattersall, 1975:234). Essentially all the traits that this taxa shared were primitive, and therefore, it could be ancestral to any or all of the other taxa, including the genus *Homo*.

A number of traits were found which separated *Australopithecus boisei* and *Australopithecus robustus* from *Australopithecus africanus*, but which allied the two 'robusts' closely together. Although a split (implying a speciation event) was recorded between the two 'robusts', it was explicitly stated that said split was arbitrarily decided upon (Eldredge and Tattersall, 1975:237). The conclusion was reached that a generalized *Australopithecus africanus* population was a good ancestral morphotype for *Australopithecus robustus*, and that the latter was then a good ancestor for *Australopithecus boisei*

It was in the year 1975 that the true age of the Koobi Fora remains was determined. The dating of the site was re-examined using the more conventional K-Ar method, and an age of 1.82±0.04 Myr was obtained (Curtis, et al., 1975: 397). This had the effect of denying the existence of *Homo* at such an early age, and again paved the way for the acceptance of *Australopithecus* as being ancestral to *Homo*.

It was in the mid-1970's that the site of Hadar in Ethiopia began to produce many of its numerous, famous fossils. The earliest indications of the area were that many taxa were present, and that they bore resemblences to the known hominids of South Africa. In fact, "on the basis of the present hominid collection from Hadar it is tentatively suggested that some specimens show affinities with *A. robustus*, some with *A. africanus* (sensu stricto), and others with fossils previously referred to *Homo* (Johanson and Taieb, 1976:297)." However, it was noted that many of the fossils found were possessed of features which were held to be more primitive than known taxa. It was only after the fossil record of the area grew even more that the new taxon, *Australopithecus afarensis* was erected.

Of particular importance was the discovery of the almost complete (40%) skeleton found in 1974. Nicknamed 'Lucy', it was the most complete known australopithecine at the time, and remains so to this day. She garnered worldwide attention, and still fascinates even today. More importantly, she provided the first real look at a rather complete, partially articulated skeleton, something almost unknown to that time.

Richard Leakey, meanwhile, had recovered more fossils, and this time had more concrete taxonomic designations for his East Rudolf finds than had been given before. He identified the presence of *Australopithecus boisei* at Koobi Fora, but then went on to claim that the validity of the species *boisei* might be fallacious. He felt that "*A. boisei* may require reconsideration as a full species and should perhaps be ranked on a subspecies basis, as a deme of the South African form *A. robustus* (Leakey, 1976a:176)." He next claimed that the gracile specimens he had from Koobi Fora, including ER1813, as well as some specimens from Olduvai, including OH24, were morphologically most similar to *Australopithecus africanus* (Leakey, 1976a:176). Finally, he attributed ER1470 to *Homo habilis*, but again, he had reservations about the existence of the taxa.

Leakey lamented the fact that various stages of evolving lineages are quite difficult to separate taxonomically, and that the designations are necessarily arbitrary. He thus suggested that only *Homo erectus* and *Homo sapiens* be retained, and that the different stages or grades of the lineage be named (Leakey, 1976a:177). This would effectively demolish *Homo habilis*, but would present a much clearer picture of the hominid lineage. His view of the genus *Homo* was quite similar to his father's; he felt that *Australopithecus* held only a very early place in human evolution, and that "the genus *Homo* will eventually be traced into the Pliocene at an age of between 4 and 6 million years, together with *Australopithecus* (Leakey, 1976a:177)."

Incidentally, Leakey believed that the Hadar remains of Johanson, particularly 'Lucy', might be considered a late *Ramapithecus*.

Support for Leakey's claim for the status of *Homo* came in the form of contemporaneous *Homo erectus* and *Australopithecus boisei* fossils at Koobi Fora (Leakey and Walker, 1976). The two were positively located in the same sediments, and strongly favored their coexistence. This was felt to be the final piece of evidence demolishing the single species hypothesis. Also, post-cranial remains were thought to add weight to the late Pliocene division of *Australopithecus* and *Homo* (Leakey, 1976b:576).

Again, Leakey stated that the 'robust' material he was recovering at Koobi Fora belonged to *Australopithecus boisei*, and again he claimed that this taxon might be no more than a subspecies of *Australopithecus robustus* (Leakey, 1976b:576). The more 'gracile' of the Koobi Fora material was thought to be similar to *Australopithecus africanus*, but it was noted that there was no convincing evidence for *Australopithecus* occurring earlier than *Homo* (Leakey, 1976b:576).

In 1976, the hominid site at the locality known as Laetolil, near Olduvai in East Africa was reopened under the direction of Mary Leakey. The fossils found at this site were apparently older than any other confirmed hominid fossils, dated at approximately 3.59 Myr in age. Mary Leakey et al. indicated that their new finds bore certain affinities with the genus *Homo*, but also possessed some primitive traits "concordant with its great age" (M. D. Leakey et al. 1976:464). It was felt that the Laetolil fossils were very early members of the genus *Homo*, though they also bore resemblences to the 'gracile' South African australopithecines (M. D. Leakey et al., 1976:466). It was also noted that the Laetolil fossils showed strong similarities to the newly discovered Hadar fossils.

As more fossils were being recovered at Omo and East Lake Turkana (formerly Lake Rudolf), the taxonomy of the australopithecines, rather than clarifying, was becoming increasingly confused. The new australopithecine finds at Omo were being placed within the taxonomic framework developed for the more southern African material. Hence, the 'robust' material being found was attributed to *Australopithecus boisei*, while the 'gracile' material showed closest affinities to *Australopithecus africanus* (Howell and Coppens, 1976). These attributions were based in large part on Howell's comparative studies at Olduvai, Lake Turkana, and the South African sites, and it was noted that they were subject to later revision (Howell and Coppens, 1976:530). They recognized 4 taxa at Omo. *Australopithecus africanus*, represented in the Usno and lower Shungura formations; it was noted that these remains might actually "represent a distinctive, though related, lower taxonomic category (Howell and Coppens, 1976:530)." *Australopithecus boisei* was found in the middle members of the Shungura Formation. As well, both *Homo habilis* and *Homo erectus* were recognized.

Supporting evidence for the younger age of the Koobi Fora remains was provided in 1977, when a detailed analysis of Suid evolution in East Africa was performed (White and Harris, 1977).

Based on faunal correlations, the Koobi Fora remains, thought to be 2.6 Myr old, were strongly associated with those from Olduvai, which had been dated quite firmly at 1.8 Myr. White and Harris therefore exclaimed that the age of Koobi Fora was not as old as was claimed, but rather of the same age as Olduvai (White and Harris, 1977:20). This essentially was in agreement with Curtis et al. (1975), when they revised the age of the important KBS Tuff. The ages of the Makapansgat finds were also considered to be older than Swartkrans, and the ages of the South African 'robust' and East African 'hyper-robust' species were approximately contemporaneous, thus removing any consideration of an ancestral-descendant relationship.

Seeking to construct a hominid phylogeny which would be both testable and falsifiable, another cladistic analysis was performed on the family Hominidae (Delson, et al., 1977). The results of this study were similar to Eldredge and Tattersall (1975). They recognized the 'robust' and 'gracile' varieties of *Australopithecus* as subgenera of that genus, and further suggested that the two 'robust' species might form a superspecies. They also again refused to accept *Homo habilis*, and instead attributed the Olduvai fossils (including OH7, the holotype) within *Homo erectus* (Delson, et al., 1977:270). It was also believed that *Australopithecus africanus* was a perfect ancestor, which means that all of its traits were primitive when compared with both the 'robusts' and with *Homo*, again implying that it was most likely ancestral to all of these.

In an earlier edition of their book *Human Evolution*, Brace and Montagu had stated that the australopithecines could easily be housed within one genus, *Homo*. However, in the 1977 edition they note that they had backed away from this view, stating that the early hominids differ enough to warrant a generic distinction from *Homo* (Brace and Montagu, 1977:285). They still only recognized one species, *Australopithecus africanus*. The difference between *Australopithecus* and *Paranthropus* was not accepted as valid, not even at the specific level. Rather, extremes of sexual dimorphism were thought to be the causal factor in the differences in size between the two groups, as well as the use of one or two specimens to typify the entire group being discussed (Brace and Montagu, 1977:289).

As regarded *Homo habilis*, it was again claimed that the Bed I Olduvai material could not be distinguished from *Australopithecus*, while the Bed II remains were very similar to *Homo erectus* (Brace and Montagu, 1977:294). Brace and Montagu chastized the Leakeys for having "taken all the more delicately constructed material and lumped it into a single category (Brace and Montagu, 1977:295)." Sexual dimorphism had been ignored, and as a result an invalid and biologically incorrect taxon had been constructed.

As time went by, studies of greater depth and analytical precision were being performed upon the australopithecines, including a greater reliance on statistical techniques. Employing a generalized distance technique to express the different rates of change in a morphological character complex, Bilsborough (1978) was able to show patterns of mosaic evolution in certain regions of the skull of the australopithecines. Mosaic evolution simply means that different characters or complexes of characters are under different selective pressures in a species, and therefore may evolve at different rates. He found that the cranio-facial proportions of the 'robusts' were in essential agreement, but clearly separate from the more 'gracile' *Australopithecus africanus* (Bilsborough, 1978:340). This indicated that there was genetic discontinuity between the two groups, but the level of that discontinuity, i.e. generic or specific separation, was a matter of taste. Although the degree of difference between the groups might be seen as warranting a generic distinction, Bilsborough chose to retain only a specific separation, stating that the weighting of the characters in a cladistic fashion might change the outcome (his was a phenetic approach). However, when discussing the essential similarity of the 'robust' species, he felt that ". . . schemes distinguishing two robust species *A. robustus* (South Africa) and *A. boisei* (East Africa) may require revision, and that the two groups are perhaps most appropriately accommodated within a single polytypic species (Bilsborough, 1978:341)."

The vast new numbers of fossils that were being discovered throughout Africa, although exciting, were also causing some concern. Tobias noted that the large influx of new fossils was outstripping proper description and analysis (Tobias, 1978:373). New problems in classification were popping up, and a number of different views of hominid phylogeny were becoming prevalent. The status of *Australopithecus* as a genus was in question (Robinson, 1961; 1963; 1968; 1972), but it was felt that it was, nonetheless, a valid, coherent taxon (Tobias, 1978:379). Indeed, Tobias was strongly convinced that a population of *Australopithecus africanus* was ancestral to the genus *Homo*, and therefore ourselves. He felt that the claims of early representatives of the genus *Homo* in East Africa were unconvincing, that the earliest confirmed evidence of the genus occurred at 1.9-2.1 Myr at Lake Turkana (formerly Lake Rudolf), around 1.85 Myr at Olduvai and at Omo, and again at Swartkrans ca. 2.0-1.5 Myr. There was no population of *Homo* anywhere which was significantly older than 2.0 Myr, and therefore *Australopithecus africanus* was "the most likely claimant to have been ancestral to *Homo* (Tobias, 1978:391)." This was in direct contrast with the views of Oxnard (1975) as well as Leakey (1971; 1972), who both held *Homo* to be so ancient as to preclude its being derived from *Australopithecus.*

Delson (1978) was among the first to apply strict cladistic methodologies to the australopithecines, although he did borrow strongly from Eldredge and Tattersall (1975). Based on his analysis, he was able to conclude that the genus *Australopithecus* was best divided at the subgeneric level, using *Australopithecus* and *Paranthropus* for the 'gracile' and 'robust' lineages respectively (Delson, 1978:538). He further stated that it might be best to group the 'robusts' together into a superspecies, owing to their extreme similarity. *Homo habilis* was recognized as a valid taxon, intermediate morphologically and perhaps phyletically between *Australopithecus cf. africanus* and *Homo cf. erectus* (Delson, 1978:538).

Employing the principle of parsimony espoused by William of Occam, Campbell again asserted a lumper's taxonomy, recognizing the minimum number of discrete lineages possible for the Hominidae (Campbell, 1978:579). As before, he recognized the genus *Australopithecus* as possessing only two species, *africanus* and *boisei*. *Australopithecus robustus* and *Homo habilis* were subsumed into

Australopithecus africanus at the subspecies level. And, within *Homo*, Campbell allowed only *Homo erectus* and *Homo sapiens*. His arguments were sometimes weak, and often difficult to follow, and it is apparent that few accepted this extreme lumping.

The influence of John Robinson was once again seen in the work of Todd Olson, beginning in the late 1970's. Of particular importance is the fact that Olson supported the view that the genus *Paranthropus* was in fact valid, and that the remaining 'gracile' australopithecine fossils should be assigned to the genus *Homo* (Olson, 1978). He preferred to view *Australopithecus* as a subgenus of *Homo*. At Swartkrans, he saw evidence of two distinct lineages, *Paranthropus robustus* and *Homo africanus* (Olson, 1978:170). He also saw a distinction between *Paranthropus robustus* and *Paranthropus boisei*, based on a cladistic analysis he performed upon their respective crania. The main conclusion reached in the paper was that *Homo* and *Paranthropus* were quite distinct genera, while *Australopithecus* was actually a polyphyletic group, characterized by symplesiomorphic characters (Olson,. 1978:174). *Australopithecus* was therefore untenable, and it was recommended that it be sunk.

It was in the year 1978 that the latest commonly accepted taxon was proposed, and as had met all new taxa since 1953, it was greeted with a storm of controversy, not yet abated even today. In the next section, a discussion of the final trend will be given, which will include one new genus, 3 new species, and the resurgence of a long ago sunk genus.

2.4 The Recent Period 1978-1995 - The Splitting Reigns Anew

The year 1978 is a significant one in the field of paleoanthropology, in that it was the year that the latest, widely accepted australopithecine species was named. The many new finds being made in the Afar region of Ethiopia, particularly at the site of Hadar, by Don Johanson and his research team were fast accumulating. These hominid fossils appeared to display a much more primitive structure than was known from the South African 'gracile' form, *Australopithecus africanus*. As more and more comparisons were made, Johanson and his research colleague, Tim White, became more and more convinced that what they were dealing with was a new species. This culminated in an article in the official journal of the Cleveland Museum of Natural History, *Kirtlandia*. In this publication, Johanson, White and Coppens (1978) named their new species *Australopithecus afarensis*.

This species was the first australopithecine species to be named on more than just a single fossil or handful of fragments. Rather, a whole suite of fossils was utilized to give a very complete diagnosis of this new taxon. These included the Hadar remains, as well as those from Laetolil in Tanzania. It was felt that the two sites were possessed of the same species. So strong was this conviction that the designated holotype, required by the ICZN for every new taxon, was a mandible from Laetolil, L.H.4. The Laetolil beds were positively associated with this new taxon.

The Hadar fossil collection as well had grown to considerable size, and included many dozens of fossils. Notable in this group was the 40% complete skeleton found in 1974 and dubbed 'Lucy' (Johanson and Taieb, 1974). Her pelvis and partial knee, along with another articulated knee found in 1973, proved with little doubt (though there were skeptics) that even the earliest known australopithecines, dated to greater then 3.0 Myr, walked bipedally and with a fully erect posture. The arguments of those who would see hominids a million years younger (e.g., *Homo habilis*) moving about in a much less efficient or advanced fashion were seriously damaged.

The selection of the Laetolil Hominid 4 fossil as the holotype provided something of a problem for the namers. It was selected since it was the only well described fossil of the group at the time, and because it was rather a distinctive, diagnostic piece (Johanson, et al., 1978:8). However, the fossils from Laetolil were originally named *Präanthropus* by Hennig in 1948, and as such, this name had precedence. Nevertheless, since the genus was named without a trivial designation, it was an invalid nomen. Subsequent to this, the fossil LH4 had been renamed *Meganthropus africanus* by Weinert (1950), and later *Praeanthropus africanus* by Senyürek in 1955. But, since the new namers did not feel the generic distinction from *Australopithecus* was warranted, they housed it within that genus, thereby avoiding *Meganthropus* and *Praeanthropus*. The trivial name *africanus* would be the next potential name, but as this name was already occupied in *Australopithecus*, a new one was designated. The species name *afarensis* was selected, as it represented the region where the bulk of the fossils were found, the Afar Triangle.

Similarities between the new taxon and others known forms (*Australopithecus africanus* and *Homo habilis*) were recognized, but it was felt that the overall character complex was different enough to warrant the new name (Johanson et al., 1978:8). The actual phylogenetic position of the new species was to be considered in subsequent papers.

Australopithecus afarensis was announced to the world with sufficient fanfare, but it was not well received by many researchers. The battle would soon be joined.

The splitting trend to be documented in this time frame was not restricted to new taxa. Old, previously discarded taxa were also to make their claims. In 1978, F. Clark Howell performed an exquisitely detailed analysis of all the known hominid taxa at the time. In this study, Howell recognized the existence of 2 genera and 7 species, which were: *Australopithecus africanus*, *A. boisei*, *A. crassidens*, *A. robustus*, *Homo habilis*, *H. erectus*, and *H. sapiens* (with three subspecies). Notable in this list is *Australopithecus crassidens*, which Robinson had officially sunk 24 years earlier into *Australopithecus robustus* (Robinson, 1954). Howell accepted this taxon, represented only at Swartkrans, as being biologically valid. This removed a significant portion of the fossils from the hypodigm of *Australopithecus robustus*, leaving behind only the Kromdraai remains to represent that species. This idea was not well received, and only a select few accepted the validity of *Australopithecus crassidens* (see below). Conspicuous by absence was *Australopithecus afarensis* which, at the time of publication, had not yet been unveiled.

A note must be added about the exclusion of Howell's work in the analysis of this current study. Although wonderfully detailed and insightful, Howell's descriptions of the species were not intended to be exclusively diagnostic of each separate species. Rather, he listed out all traits known for each one, regardless of whether said trait refers to one or more species. His traits do not necessarily refer to one and one only species, and as such would add considerable confusion to this work if included. They would add a large number of traits to the compiled lists which were never intended to be diagnostic of a species. It is firmly believed that since Howell's work was a compilation of the masses of morphological traits that had been put forward in the past for each of the australopithecine species, the review done for this current thesis (i.e., this chapter) will uncover each and every trait utilized by Howell, and no information will be lost.

One of the first to comment on the new species *Australopithecus afarensis* was Noel Boaz (1979). His first reaction was cautious, and he felt that, "while this new taxon may eventually prove to be warranted, several problems prevent its immediate acceptance (Boaz, 1979:77)." One of these problems was the uncertainty that arose from an incomplete knowledge of the range of variation allowable within *Australopithecus africanus*. Another was the lack of comparable anatomical parts between *Australopithecus africanus* and *Australopithecus afarensis*, including a paucity of cranial elements in the latter, and a dearth of similar post-cranial elements in the former. Boaz concluded that "even though *A. afarensis* is suggested to be a more primitive australopithecine species, Hadar (dating from 3.3 to 2.9 Myr BP) overlaps in time with available age estimates of *A. africanus* from South Africa (ca 3 Myr BP). This fact, coupled with close morphological similarities with *A. africanus*, brings into question the appropriateness of the new taxonomic name (Boaz, 1979:77)."

When discussing the taxonomic validity of *Homo habilis*, Boaz stated that close morphological similarities between it and *Homo modjokertensis* made the two taxonomically synonymous. The rule of priority would therefore make the trivial designation *Homo modjokertensis*, as it was the first taxon named (Boaz, 1979:78). The 'robust' australopithecines were seen as being valid separate taxa, based mainly on Tobias' in-depth monograph on OH5 (1967b).

In 1979, based on the recent finds at Hadar, Johanson and White provided a systematic re-assessment of the early hominids, as well as their reasoning behind naming a new species. Rather than considering *Australopithecus afarensis* to be an ancestral form in the *Australopithecus africanus->Homo habilis* lineage, they felt that *Australopithecus africanus* itself was not at all in the direct line to *Homo*. Instead, they saw *Australopithecus africanus* as an evolutionary offshoot leading to the 'robust' lineage, and ultimate extinction without issue (Johanson and White, 1979a:328). *Australopithecus afarensis* was the basal australopithecine stock which split into two lineages, one leading to *Homo*, the other leading to *Australopithecus robustus/boisei* (Johanson and White believed these two 'robust' groups to be conspecific; 1979a:327, fig.9). This was a radical re-interpretation of hominid phylogeny, and meant that the original *Australopithecus* species, *africanus*, was relegated to the status of an evolutionary dead end. This did not sit well with many of their colleagues.

Other fascinating new discoveries in paleoanthropology were also being made at this time, and public interest was again reaching a fever pitch. Mary Leakey had discovered at the site of Laetoli (formerly known as Laetolil) numerous animal footprints left in the soft ash of an ancient volcanic eruption (Leakey and Hay, 1979). Most amazing of these footprints were the ones made by undeniable hominids; it was erect, bipedally walking animals which had left these behind. Through an extraordinary feat of preservation, the footprints were shielded for posterity, and they afforded a remarkable look at the biomechanics of the stride of our ancient ancestors. They also provided the most reliable dating for early hominids ever recorded, as the footprints were placed within the actual ash which would be used for the dating procedure, as it was deposited, instead of being merely closely associated with said ash as most fossil dates are. The date arrived at for this ash was 3.6-3.75 Myr (Leakey and Hay, 1979:318). The foot that made the prints was quite human-like, with an extended big toe, positioned just like a human. It was concluded that at earlier than 3.6 Myr, the hominids at Laetoli had achieved a fully upright, bipedal and free-walking gait (Leakey and Hay, 1979:323).

It was noted that the footprints were most likely made by members of the taxon *Australopithecus afarensis* (White, 1980:175). White also noted the mosaic form of hominid evolution evinced by these footprints. Although *Australopithecus afarensis* had a very small brain, it was nonetheless fully bipedal over 3.6 Myr, with what was interpreted to be a post-cranial anatomy very similar to our own. The transmission of propulsive forces to the ground (Day and Wickens, 1980:385), and the weight distribution (Leakey, 1981) were also carried out in a manner very similar to modern humans

The first direct attacks on the newly named *Australopithecus afarensis* were disappointingly weak. Day et al. (1979) chose to focus on somewhat minor taxonomic points, pointing out some rather niggling details of possible confusion in the proposed new taxon, none of which did any damage whatever to the actual naming of the species. Leakey and Walker (1979) took issue with the phylogeny that Johanson and White (1979a) erected, rather than the new species itself. They claimed that some of the fossils which Johanson and White had attributed to early *Homo* (OH13, OH24) actually represented late surviving *Australopithecus*, and therefore the phylogeny as regarded the relationship between *Australopithecus* and *Homo* required revision (no mention was made of the actual species *Australopithecus afarensis*).

There were also supporting arguments for the new species. McHenry and Corruccini (1979) indicated that based on their analysis of mandibular molar morphology, made on crown component measurements, the new species, as well as the phylogenetic implications raised by Johanson and White (1979a), were correct. The two lineage model with *Australopithecus afarensis* at the base, and *Australopithecus africanus* specializing towards the 'robust' species was supported, and it was noted that "the morphological distances show that less change is necessary to connect *A. afarensis* to *H. habilis* than to relate *A. africanus* to *H. habilis* (McHenry and Corruccini, 1979:1104)."

In a reply to the above articles (the three above articles were published together, along with this reply), Johanson and White (1979b) pointed out many of the weaknesses in the criticisms, and again asserted the scientific validity of their recently proposed (1979a) phylogenetic scheme.

An anonymous editorial in the journal *Nature* also severely criticized the new species of Johanson et al. (1978). The reviewer felt strongly that "their [Johanson et al. (1978)] success in demonstrating the morphological distinctiveness of *A. afarensis* is by no means clear" and that ". . . very few characters of *A. afarensis* are not also found in *A. africanus* (Anonymous, 1979:400)." The reviewer also attacked White and Johanson (1979) for including the specimens from Makapansgat in their comparative grouping of *Australopithecus africanus* since it was not clear whether the Makapansgat fossils were actually of the 'gracile' or 'robust' clade. It was concluded that "thus, there are very few features said to be characteristic of *A. afarensis* which are, in fact, distinctive of that group (Anonymous, 1979:401)."

By this point, the Omo Research Expedition had been in operation for some time, and preliminary results were presented by Coppens in 1980. The fossils found had been attributed to various taxa in most cases, but there were some anomalous finds as well. In the Usno Formation, and the lower part of the Shungura as well, remnants were found which were attributed to *Australopithecus cf. africanus*, although it was noted at this point that their similarities might lay with the new taxon, *Australopithecus afarensis* (Coppens, 1980:212). It was also noted that there were many teeth from the upper Shungura members which seemed to belong to *Australopithecus africanus*. From some of the oldest (2.2-2.5 Myr) members of the Shungura, right down to some of the youngest (1.1 Myr) members, specimens firmly ascribed to *Australopithecus boisei* were found. It was in this taxon that the mandible Omo 18-1967-18, type specimen for the defunct species *Paraustralopithecus aethiopicus*, was placed. There were also fragments which most closely resembled *Homo habilis* found in members G and H of the Shungura Formation.

The amounts of variation recognizable in the genus *Australopithecus* were still not fully known. While he accepted tentatively the separation of *Australopithecus* into four species, Kennedy (1980) asserted that ". . . it is by no means clear that the two robust forms, *A. robustus* and *A. boisei*, are distinctive from each other at the species level. They could well be geographic variants or subspecies of one taxon. Moreover, the gracile forms, *A. africanus* and *A. afarensis* may not warrant separate species since they share many features (Kennedy, 1980:215)."

By far the most ardent critic of the new taxon *Australopithecus afarensis* was Phillip Tobias of the University of the Witwatersrand in Johannesburg, South Africa. The status of the species was never accepted, and the fossils themselves were considered to be part of *Australopithecus africanus*. Even before he was able to study *Australopithecus afarensis* in any detail, Tobias felt that, based on the descriptions and measurements provided, "there is no evidence from Africa (or anywhere else) of the existence in this earlier phase (i.e. before 2.5 Myr) of any hominid or group of hominids differing so markedly from the sample range of *A. africanus* as to justify the postulate that a second species of hominid was in existence at the time (Tobias, 1980a:105)." The amount of variation seen prior to this date (i.e. 2.5 Myr) did not require more than one species. However, after this date, a large amount of variation was seen, and numerous lineages burst onto the scene in what seemed like "explosive evolution" (Tobias, 1980a:110). Suddenly we find *Homo habilis* continuing in the 'gracile' mode with certain morphological and quite probably ethological differences, while the 'robust' australopithecines also make their appearance. Still, prior to this 2.5 Myr date, Tobias saw room for only one lineage. The materials from Laetoli (and by extension Hadar) formed no more than a new subspecies, *Australopithecus africanus tanzaniensis* (Tobias, 1980a:86). They were certainly not ancient representatives of the genus *Homo* as Mary Leakey et al. (1976) had felt.

After many years of careful analysis, Richard Leakey was able to decide exactly which taxa he had found at Lake Turkana (formerly Lake Rudolf), but again was willing to do so only to the generic level. The large toothed 'robust' specimens he referred to the genus *Paranthropus*, noting that similar hominids were found at Olduvai, and were called *boisei* (presumably he felt these too belonged in *Paranthropus*) (Leakey, 1980:30). The more advanced of the 'gracile' specimens were attributed to *Homo*, some being *erectus*, others *habilis*. Of the more primitive 'graciles', Leakey believed them to belong to the genus *Australopithecus*, but although he noted affinity with *Australopithecus africanus*, he refused to place them in this taxon (Leakey, 1980:30). Essentially Leakey felt there were three taxa, all distinguished at the generic level. The evidence provided was scanty at best, and the anatomical details he provided would have allowed almost any ape into the taxa he described.

After naming his new species *Australopithecus afarensis*, Johanson (1980) again reiterated in greater detail some of the points he had made. He was quite clear that he did not believe the new taxon to be generically distinct from *Australopithecus*, and rejected any possibility of such a proposal (Johanson, 1980:57). When it came to *Australopithecus africanus*, however, the picture was changed somewhat. Johanson felt that "examination of specimens assigned to *A. africanus* in South Africa reveals that they are morphologically intermediate between *A. afarensis* and 'robust' australopiths (Johanson, 1980:61)." They were now an evolutionary offshoot, leading to extinction. Johanson admitted that it was "impossible to distinguish each specimen of *A. afarensis* from all specimens included in the South African 'gracile' australopith sample (Johanson, 1980:61)," but that the new phylogenetic scheme proposed (Johanson and White, 1979) placed *Australopithecus africanus* on the line to the 'robusts', and therefore out of the role of human ancestor (Johanson, 1980:63). *Australopithecus afarensis* and *Homo habilis* on the other hand showed some dental similarities which cladistically linked them and excluded *Australopithecus africanus*. A number of characters which separated *Australopithecus afarensis* and *Australopithecus africanus* were listed out.

As mentioned earlier, Phillip Tobias was never able to accept the validity of *Australopithecus afarensis*, and was especially critical of the new phylogeny that placed *Australopithecus africanus* on a side branch leading to the 'robust' australopithecines. He provided a very strong criticism of the new species, as well as an alternative point of view as to the true position of *Australopithecus afarensis* (1980b).

Tobias first noted the taxonomic confusion that had surrounded the Hadar finds. Originally it had been claimed that *Homo* and both 'gracile' and 'robust' *Australopithecus* were represented at Hadar (Johanson and Taieb, 1976). This was later recanted, but the existence of 'robust' elements at Hadar would be very important as will be seen later. Tobias was firmly convinced that the hominids from Hadar and Laetoli were not a new species, and that "in a word *A. afarensis* cannot be separated from *A. africanus* on the characteristics that have been adduced as the diagnosis (Tobias, 1980b:9)." To prove this, he went systematically through 8 cranial, 5 mandibular, and 8 dental traits that Johanson et al. (1978) had claimed defined their new species. Of these, none were able to separate *Australopithecus afarensis* from *Australopithecus africanus* or in certain cases *Australopithecus boisei*. The features studied were not exclusive to the new taxon, and therefore "the 'diagnosis' of '*A. afarensis*' by Johanson et al. (1978) has proved to be not diagnostic; and working systematically through the remaining half-dozen enumerated traits, I have been lead to the same conclusion about them (Tobias, 1980b:9)." Tobias felt that no features at all were capable of separating out *Australopithecus afarensis* from *Australopithecus africanus*.

Tobias further argued that the pooling of the Hadar and Laetoli fossils might not be legitimate, or that it at least had not yet been proven sound (Tobias, 1980b:10). He cited both the wide chronological gap (as much as 830,000 years) as well as the geographical separation (1600 km). He found the Laetoli material to be morphologically quite similar to the South African finds, while the Hadar teeth were seen to be a little bit smaller.

The phylogenetic system which had been erected by Johanson and White (1979) came under fire next. Tobias first criticized the two for underestimating the age of the South African sites in spite of numerous estimates which made it much older than Johanson and White felt. The older dating of the South African sites made the new phylogeny much less supportable.

As to the supposed 'robust' elements seen in *Australopithecus africanus* which placed it in the 'robust' lineage, Tobias argued that a large over-generalization had been made about an entire species based on a few references to Makapansgat (Tobias, 1980b:13). Some of the fossils from this site had been called 'robust' by certain authors, and as a result of this, Johanson and White saw *Australopithecus africanus* leading down the trail to 'robustness'. Tobias argued that the traits mentioned were highly variable, and were likely just extremes of variation for the species. He also argued that the older Makapansgat fossils possessed 'robust' traits which were not seen at the younger Sterkfontein, and which thus precluded the phylogenetic interpretation made by Johanson and White. Also, the claims for the presence of 'robust' elements at Hadar came back to haunt Johanson and White, as they emphasized the fact that polymorphic expressions of certain traits at both Hadar and Makapansgat (approximately contemporaneous sites) could display 'robust' elements (Tobias, 1980b:14).

Tobias thus concluded that *Australopithecus afarensis* was not a valid taxon. Rather, the two sites, Hadar and Laetoli, at best represented new subspecies. For the Laetoli specimens he recommended the name *Australopithecus africanus afarensis*, and for the Hadar remains *Australopithecus africanus aethiopicus*. *Australopithecus africanus* was the basal hominid, and the direct human ancestor.

The taxonomic unity of the species *Australopithecus afarensis* was contested on other grounds as well. In a cladistic study of the basicranium of the primates, Olson (1981) was able to establish that there were in fact two taxa represented at Hadar, much as the initial reports (Johanson and Taieb, 1976) had indicated. Olson believed that the partial skull, AL333-45 (a member of the so-called 'first family') was in fact a 'robust' australopithecine, and a member of the genus *Paranthropus* (Olson, 1981:101). It must be noted that Olson accepted Robinson's distinction between the two hominid genera *Paranthropus* and *Homo* as being essentially correct. Since Olson was removing *afarensis* from *Australopithecus*, and since the type specimen of the new species had been the Laetoli mandible LH4, which was first named *Meganthropus africanus* by Weinert (1950), *africanus* held priority, and therefore the new taxon had to be named

Paranthropus africanus (Olson, 1981:118). Olson felt that the new species was distinct from the other known 'robust' species.

Most of the Hadar materials, in fact, were placed within *Paranthropus* by Olson. There were, however, some 'gracile' specimens which could not fit there, notably AL288-1, Lucy. Olson believed these to be among the earliest representatives of the genus *Homo* (Olson, 1981:123). Exactly what species they represented was unknown at the time, and the taxon was simply referred to as *Homo spp. indet.* Olson theorized that approximately 4.5-5.0 Myr, the hominid lineage split into *Paranthropus africanus* and *Homo spp. indet.*, and the two subsequently followed their own evolutionary pathways, one leading to modern humans, the other to extinction.

The variation that was to be allowed for early populations of hominids was apparently ignored in the naming of *Australopithecus afarensis*. Tobias (1981) noted that the different australopithecine sites in Africa were separated by thousands of miles, and "over such vast distances, it is to be expected that early hominids would have been subject to geographical variation, even as other mammals are (Tobias, 1981:45)." Even within certain sites, such as Hadar, a long chronological sequence was known, which would add significantly to the amount of variation seen. The pooling of Hadar and Laetoli was not acceptable to Tobias until more accurate descriptions and measurements of the Hadar remains had been published. Since the two sites did show morphometric differences, and since they were over 800,000 years separate at their chronological mid-ranges, Tobias felt that they were more likely to be separate subspecies of *Australopithecus africanus* (Tobias, 1981:46).

Tobias (1981) again criticized Johanson and White (1979) for both mis-dating the South African sites as well as misrepresenting the species as possessing 'robust' elements, when it was only a few Makapansgat remains, and not any of the Sterkfontein remains, which displayed these features. He indicated that the Laetoli and Hadar fossils could not be separated morphologically from *Australopithecus africanus*, and therefore recommended that the name *Australopithecus afarensis* be officially suppressed as allowed by the ICZN. He firmly stated that "both procedurally, comparatively and morphometrically, it does not appear that a case has been established for the claims that the hominids of Laetoli and Hadar represent a single population and that that population has been sampled from a new species of early hominid (Tobias, 1981:47)."

White, Johanson and Kimbel responded to the charges of Tobias in 1981. In their article, they presented quite detailed analyses of the known australopithecine fossils from both South Africa and eastern Africa. *Australopithecus afarensis* was compared to *Australopithecus africanus* in a number of cranial, mandibular and dental traits, and was determined to be both distinguishable, and more primitive (White, et al. 1981:467). *Australopithecus africanus* was also determined to be a very likely ancestor of the 'robust' australopithecines, specialized in this direction to the extent that it was removed from the human lineage. They also believed that "morphologically, the Hadar and Laetoli samples are essentially indistinguishable (White, et al., 1981:448)," and therefore the pooling of the two sites into one species was perfectly justifiable.

The ages of the South African sites were also reconsidered, and it was held that "biostratigraphic evidence indicates an age of between 2.0 and 3.0 Myr for known *A. africanus* in South Africa (White, et al. 1981:430)." This age was apparently younger than other estimates of between 3.0 and 2.5 Myr (Tobias, 1981). Older dates for the South African fossils would make the case for ancestorship of *Australopithecus afarensis* weaker. However, White et al. felt that ". . . it is clear that the Transvaal's *A. africanus* postdated most East African *A. afarensis* by about 0.5 Myr. It was therefore chronologically intermediate between *A. afarensis* and *A. robustus* + *A. boisei* whose earliest representatives are known from deposits about 2.2 Myr old (White, et al., 1981:450)."

When reconsidering the status of *Australopithecus africanus*, it was felt that "the morphological differences between these [Laetoli and Hadar] fossils and South African *A. africanus* are equivalent in magnitude to those employed by vertebrate paleontologists in the definition of species. A subspecific designation within *A. africanus* for the Hadar and Laetoli hominids is rejected by these differences (White, et al. 1981:466)." The differences mentioned were the detailed anatomical ones listed out in the article. It was believed that combining the Hadar and Laetoli fossils with *Australopithecus africanus* "would obscure the real and evolutionarily significant differences between them (White, et al. 1981: 466)." As such, *Australopithecus afarensis* was held to be a valid biological taxon, ancestral to both *Homo habilis* and *Australopithecus africanus*, the latter of which was in turn exclusively ancestral to *Australopithecus robustus* and *Australopithecus boisei.*

One interesting side-note here involves the 'robust' australopithecines. In the discussion of the phylogenetic status of the genus in general, it was noted that "South African *A. robustus* and East African *A. boisei* are often considered together in this publication, since the question of whether or not these taxa are conspecific remains unresolved (White, et al. 1981:445; footnote)." Still, the authors did proclaim that ". . . evidence for a specific distinction between contemporary *A. robustus* and *A. boisei* is mounting (White et al., 1981:467). It would await the work of Rak (1983) for the separation of these taxa to become codified, as will be seen below.

Nevertheless, there were other rumblings of significant differences between the two groups of australopithecines. In a study of the usefulness of tooth measures and tooth morphology, it was stated that "if canine base area and molar crown area are considered there is considerable overlap between *Australopithecus africanus* and *Australopithecus (Paranthropus) robustus* whereas there is little or no overlap between the ranges of *Australopithecus africanus* and *Australopithecus (Paranthropus) boisei* (Wood, 1981:65)." Thus tooth area measures were able to distinguish in some manner between the two groups of 'robust' australopithecines. Unfortunately, it was also noted that "it is clear from this review that there is sufficient overlap between the gracile and robust australopithecines in simple tooth dimensions for tooth size alone to be ineffective as an indicator of taxonomic affinity (Wood, 1981:74)." It is unclear whether this ineffectiveness was isolated to distinctions between the 'robust' and 'gracile' taxa, or whether it also held for intertaxic distinctions between the two 'robust' groups.

In an analysis of the dental microwear patterns of the deciduous dentition of the australopithecines, Grine (1981) noted that ". . . it would appear that the 'robust' australopithecines of South Africa were eating harder, more resistant (and perhaps smaller) food objects than the South African 'gracile' australopithecines (pp. 223)." Based on this he concluded that "the East African 'robust' australopithecine is derived from the South African, and that the Swartkrans 'robust' is more specialized (e.g. shows a number of apomorphic characters) than the Kromdraai australopithecine (Grine, 1981:223)." He argued against the thought that the two 'robust' species were actually only members of a single species or superspecies (cf. Tobias, 1968). Grine considered "the eastern African, the Swartkrans and the Kromdraai 'robust' australopithecines to be biologically distinct - probably at the species-specific levels - and that all represent an environmentally mediated adaptive shift from the 'gracile' australopithecines of South Africa, *A. africanus* . . . (Grine, 1981:223)." Essentially he was advocating the reinstatement of *Australopithecus crassidens* as a valid biological species alongside *Australopithecus robustus* and *Australopithecus boisei.*

As is characteristic of the field of paleoanthropology, differing interpretations of the fossil morphology created differing phylogenies. In a study of the cranial venous system, Falk and Conroy (1983) noted that all 'robust' australopithecines displayed an enlarged accessory sinus complex of blood drainage from the brain.

The exact same drainage system was also discovered in all known *Australopithecus afarensis* skulls. The phylogenetic significance of this trait was duly noted, and the conclusion was reached that *Australopithecus afarensis* was actually a member of the 'robust' lineage. It was pointed out that Olson (1981) had independently come to the same conclusion, when he regarded the AL-333-45 as being a 'robust' skull, based, in his study as well, on the basicranium. The authors felt that "the view that *A. afarensis* (with an enlarged accessory complex) gave rise to *A. africanus* (with a modern looking transverse-sigmoid complex) which in turn gave rise to *A. robustus/boisei* (again with an enlarged accessory complex) is therefore unlikely (Falk and Conroy, 1983:780)." This essentially removed *Australopithecus africanus* from the 'robust' lineage, and appeared to negate the phylogeny erected by Johanson and White (1979) and White et al. (1981).

This interpretation received some support by the analysis of Holloway (1983) on the cerebral endocast patterns of *Australopithecus afarensis*. Again, the patterns of the venous drainage systems of *Australopithecus afarensis* were seen to be similar to *Australopithecus robustus* and *Australopithecus boisei*, while *Australopithecus africanus* did not show the characteristic pattern (Holloway, 1983:422). His conclusion was different from that of Falk and Conroy (1983) and Olson (1981) in that he apparently did not feel the presence of this drainage system indicated that *Australopithecus afarensis* was in any way a member of the 'robust' lineage. Rather, he felt that they had not yet located the earliest 'robust' australopithecines. However, he did deny the phylogenetic scheme proposed by Johanson and White (1979), and the evolutionary split of the 'robust' lineage from *Australopithecus africanus* (Holloway, 1983:522).

This pattern of cranial blood drainage was also noted by Tobias (1967) in the OH5 cranium from Olduvai. Following the work of others (Falk and Conroy, 1983; Holloway 1983), Tobias (1983) also asserted the presence of the accessory marginal sinus in the Hadar finds. He reminded his readers that Johanson had also noted certain 'robust' elements in the Hadar materials, but had subsequently dismissed them. The 'robust' pattern was nevertheless seen in *Australopithecus afarensis*, while both *Australopithecus africanus* and *Homo habilis* lacked it (Tobias, 1983:117). The conclusion seemed inescapable that if Hadar materials were the remains of a species other than *Australopithecus africanus*, they represented a 'robust' form.

Kimbel (1984) replied to this scheme by analyzing the venous sinus drainage system of the skull of modern humans as well as fossil hominids. He found that the trait was highly variable in human populations, and also that the function of the accessory occipital-marginal was adaptively equivalent to the transverse-sigmoid sinus pattern (Kimbel, 1984:243). The trait was thus held to be adaptively neutral, and as such it was felt that it would not be strange to find disjunct distributions of such a character state; the character state would mimic synapomorphy, but would in fact be simply a case of parallelism (Kimbel, 1984:261). Kimbel concluded that "viewed in this light, alternate venous sinus drainage patterns have no valence in broader taxonomic and phylogenetic contexts (1984:261)." Instead, the large number of morphological features which placed *Australopithecus afarensis* at the base of the hominid radiation, ancestral to both *Homo habilis* and *Australopithecus africanus*, provided significant evidence that the venous sinus drainage pattern evidence was of limited utility.

Since the hypodigm of *Australopithecus afarensis* contained several well preserved post-cranial elements, analysis of the form of locomotion of the species was possible. Based on comparative anatomy of the australopithecines as well as apes and modern humans, Stern and Susman (1983) and Susman, Stern, and Jungers (1984) were able to conclude that *Australopithecus afarensis* engaged in significant amounts of arboreal behavior. The structure of the postcranial bones indicated that the adaptation of the animals to terrestrial bipedalism was incomplete, and that it probably spent no small degree of time on the trees. *Australopithecus afarensis* was called the 'missing link', in that it possessed both human-like and ape-like morphology and presumably behavior (Stern and Susman, 1983:314).

This hypothesis was strongly contested in the following years, based on analyses of the individual bones of the foot, and their relations to modern humans and primates. In a study of the talocrural joint, it was noted that in every functionally significant feature, *Australopithecus afarensis* was fully bipedal (Latimer et al., 1987:155). The calcaneus of *Australopithecus afarensis* also pointed to complete adaptation to bipedalism (Latimer and Lovejoy, 1989), as did the metatarsophalangeal joints (Latimer and Lovejoy, 1990a), and the hallucal tarsometatarsal joint (Latimer and Lovejoy, 1990b).

In all cases, the anatomical features studied were fully able to significantly separate out the bipedal from the quadrupedal animals. The claim for partial arboreality on *Australopithecus afarensis* appeared to have been severely weakened.

The phylogenetic scheme erected by Johanson and White (1979) and White et al. (1981) was contested by Wolpoff (1983) based on the actual traits used to separate *Australopithecus afarensis* specifically from *Australopithecus africanus*. He noted that "the very case that establishes *Australopithecus afarensis* as a distinctly more primitive australopithecine species, also reveals *Australopithecus africanus* to possess a suite of derived features shared with early members of the lineage leading to *Homo sapiens* (Wolpoff, 1993:118)." The best explanation for the similarities between *Australopithecus africanus*, *Homo habilis* and the 'robusts' was that *Australopithecus africanus* was the last common ancestor of both.

Others as well noted the similarities shared between *Australopithecus africanus* and *Homo* (Boaz, 1983). Boaz was unable to accept the new species *Australopithecus afarensis*, claiming that ". . . South African *A. africanus* represents the populations descendent from earlier, slightly more primitive *A. africanus* [i.e., *A. afarensis*] and ancestral to early *Homo* (Boaz, 1983:713)." For Boaz, the phylogenetic scheme erected by Johanson and White (1979) for *Australopithecus afarensis* had a problem, in that "a hypothetical phylogenetic connection between *A. afarensis* and *Homo*, disregarding *A. africanus*, has the disadvantage of postulating a substantial temporal, as well as morphological gap (Boaz, 1983:713)." Rather, *Australopithecus africanus* was both temporally and morphologically intermediate, and therefore quite acceptable as the last common ancestor. The morphologically slightly more primitive *Australopithecus afarensis* was actually just a slightly more primitive version of *Australopithecus africanus*, and not a new species at all.

Boaz concluded that "differences between Hadar-Laetoli and South African *Australopithecus* samples (if not due to individual variability) can be understood as evolutionary change within the *Homo* lineage" and that "the most "robust-like" of the South African sample, at Makapansgat, occurs earlier than the less robust *A. africanus* (thus not supporting a trend toward greater 'robusticity') (Boaz, 1983:714)." *Australopithecus africanus* itself was not trending towards 'robusticity'. *Australopithecus africanus* showed many similarities to *Homo*, as could be seen in the controversial attributions of various fossils to the two genera (e.g., KNM-ER1470, KNM-ER1813, OH24).

Despite the arguments of many authors (Boaz, 1979, 1983; Day, et al. 1979; Kennedy, 1980; Olson, 1981, 1985; Tobias, 1980a,b, 1981, 1983), the status of *Australopithecus afarensis* as a valid taxon was soon entrenched. It could be noted that by 1983, major consensus had been achieved on this point. A symposium held on the subject of ape and human ancestry confirmed this, with all but one contributor accepting the biological validity of the taxon (Ciochon, 1983:786).

The year 1983 also marked the publication of *The Australopithecine Face*, by Yoel Rak, a painstakingly performed and wonderfully illustrated volume on the structure of the faces of our australopithecine ancestors. This highly influential book was the result of Rak's doctoral dissertation on the subject, and it set the standard as regards the taxonomy of the australopithecines still accepted today. The taxonomic scheme worked out by Rak by studying the facial morphological minutiae of the genus *Australopithecus* has held until today, and most subsequent works dealing with the taxonomy of the hominids turn to it in search of support of the accepted taxonomic status.

At the outset of the book, Rak accepted the existence of four australopithecine species, *Australopithecus afarensis*, *Australopithecus africanus*, *Australopithecus robustus*, and *Australopithecus boisei*. The validity of this taxonomy was to be confirmed throughout the study. He took note of the different controversies that had sounded in the past, and attempted to address each of them in the book. Particularly, Rak paid attention to the claims that: 1) *Australopithecus afarensis* does not differ sufficiently from *Australopithecus africanus* to be a separate species, 2) *Australopithecus boisei* and *Australopithecus robustus* are not different enough to warrant specific distinction, 3) the 'robust' species represent a separate genus, *Paranthropus*, and 4) the heavily and lightly built hominids actually represent only one dimorphic species (Rak, 1983:10).

The results of the meticulously performed study indicated that, in fact, all four species were quite valid. Also, the status of *Paranthropus* as a valid genus was unwarranted. The single species hypothesis was also demolished, as the faces of all species were very distinct in a number of features.

A problem that exists with this book is that since so many of the facial minutiae are autapomorphic, that is, derived characteristics representative of only one species, they are impossible to reproduce, and it is thus impossible to determine their validity using an outgroup comparison. The danger in this is that any tiny little feature, regardless of potential functional irrelevance, might be postulated as denoting a species, and when numerous of these tiny differences are added together, a biologically invalid species may be described as being a good species. A check on this, and one which unfortunately was beyond the scope of this study, might be to search for facial morphological minutiae on extant primates like the chimpanzees, not to determine whether the same features noted by Rak are capable of separating them out (since they are autapomorphic and as such not replicable in any other species) but, rather, if the idea that certain minute facial characteristics are capable of separating out modern biological species is realistic.

In his conclusion, Rak claimed that ". . . almost every aspect of the *A. africanus* face indicates that the species as a whole had already embarked on the evolutionary course leading to the robust australopithecines (Rak, 1983:120)." He thus agreed with Johanson and White (1979) that *Australopithecus africanus* was an evolutionary offshoot, leading to 'robustness' and eventual extinction. Since *Australopithecus afarensis* exhibited none of the facial features of the 'robust' lineage, and since it existed prior to *Australopithecus africanus*, Rak considered it to be the 'perfect ancestor' (Rak, 1983:120). It was generalized enough to be ancestral to both the later australopithecines and the genus *Homo*.

Australopithecus boisei was considered to be the most evolved of the *africanus* -> *robustus* -> *boisei* lineage, and it was held that

Australopithecus robustus and *Australopithecus boisei* represented good species (Rak, 1983: 121). They were geographically isolated variants of a single lineage, but nonetheless, the morphological distinctions of the face were sufficient to imply a different adaptation, and therefore warrant a specific distinction. The topography of the face of *Australopithecus robustus* was seen to be extremely complex, much more so than that of *Australopithecus boisei.*

Grine (1984) elaborated on his earlier (1981) study of deciduous molar microwear, noting significant differences between *Australopithecus africanus, Australopithecus robustus,* and *Australopithecus crassidens* in occlusal facet orientation (pp.527). Nonetheless, it was noted that "despite the apparent differences in Phase I facet inclination on *A. robustus* and *A. crassidens* molars, the microwear details evinced by these crowns are very much alike (Grine, 1984:529)." Grine concluded that the 'robust' South African homindis were processing "qualitatively different (i.e. harder) items than *A. africanus* (Grine, 1984:532)."

In a study of the relation of postcanine teeth to overall body size, McHenry (1984) noted that there was a positive allometric trend from *Australopithecus afarensis* to *Australopithecus africanus* to *Australopithecus robustus*, whereas there was a negative trend within the genus *Homo*. This was seen as possible confirmatory evidence that *Australopithecus afarensis* was the last ancestor of *Homo*. However, this conclusion was rejected in favor of *Australopithecus africanus* being the last ancestor, based upon a cladistic analysis performed by the Skelton, McHenry and Drawhorn

(1984) which would subsequently be elaborated upon (see below). It was noted that for *Australopithecus afarensis* to be the last ancestor of *Homo*, a long list of approximately 20 traits would have to evolve independently in *Homo* and *Australopithecus africanus*, while for *Australopithecus africanus* to be the last ancestor of *Homo*, a suite of traits regarding post-canine megadontia would have to undergo evolutionary reversal (McHenry, 1984:303). McHenry believed that the evolutionary reversal was more parsimonious, and that the many traits shared by *Australopithecus africanus* and *Homo habilis* to the exclusion of *Australopithecus afarensis* involved several functionally independent complexes, making parallel evolution less likely (McHenry, 1984:303).

Further support for the ancestral status of *Australopithecus africanus* was provided using cladistic as well as character compatibility analyses (Yaroch and Vitzthum, 1984). It was concluded that the last common ancestor of *Homo* and *Australopithecus boisei* was very similar to *Australopithecus africanus*, and highly derived from the *Australopithecus afarensis* state, which would therefore make *Australopithecus africanus* the best, last ancestor of *Homo* (Yaroch and Vitzthum, 1984:237).

Since the cranium of *Australopithecus afarensis* was relatively unknown, being represented by only a collection of fragmentary remains, Kimbel et al. (1984) undertook to create a composite reconstruction of the species' skull, using a number of the fragments they had from Hadar. Based on this reconstruction, they were able to perform a cladistic analysis on the hominids, and concluded again that *Australopithecus afarensis* was ancestral to all other hominids, while *Australopithecus africanus* was derived in the direction of the 'robust' lineage (Kimbel, et al., 1984:383). They clearly stated that "in the cranium, jaws, and teeth *A. afarensis* exhibits a morphological pattern that we interpret as primitive for the Hominidae. *Homo habilis* retains a number of these primitive features for which *A. africanus*, *A. robustus*, and *A. boisei* share derived character states, particularly in the masticatory apparatus (Kimbel, et al., 1984:337)." They also felt there was no support for the claims of Olson that Hadar, particularly AL333-45, contained 'robust' elements.

Further evidence of the primitiveness of *Australopithecus afarensis* was provided in a study of the asterionic region of the cranium (Kimbel and Rak, 1985). Asterion was defined as the confluence of the lambdoidal, parieto-mastoid, and occipito-mastoid sutures (Kimbel and Rak, 1985:32), and it was noted that "the pronounced differences between the asterionic regions of *A. afarensis* and other early hominids and the near identity of the *A. afarensis* morphology to that of the extant apes must be taken into account in the taxonomic evaluation of this Pliocene hominid (Kimbel and Rak, 1985:51)." *Australopithecus boisei* was seen as markedly different in this region from *Australopithecus afarensis*, and this point was used to further argue against Olson (1981) and his claims for similarities between the two taxa in the mastoid region (asterion in hominids is quite close geographically to the mastoid region). The lack of development of a large asterionic region in *Australopithecus africanus*, which implied a greater reliance on the development of the anterior part of the temporalis muscle, was contrasted with *Australopithecus afarensis*, which showed extensive development at asterion, and thus a stronger development of the posterior part of the temporalis muscle. This difference implied a different masticatory apparatus, and this in turn was thought to be of "paramount importance in view of doubts expressed regarding the specific distinctiveness of *A. afarensis* and *A. africanus* (Kimbel and Rak, 1985:51)."

As well, it was noted that *Australopithecus africanus* and *Homo* specimens shared a similar asterionic region morphology. These were interpreted as being indicative of different developmental and functional backgrounds, rather than a phylogenetic relationship (Kimbel and Rak, 1985:53). Although *Australopithecus africanus* could not be excluded from the ancestry of *Homo* based on this study, its asterionic region development provided a "logical link between the apelike asterionic region of *A. afarensis* and the unique temporo-parietal overlap of *A. boisei* (Kimbel and Rak, 1985:53)."

In 1985 a major conference was held at the American Museum of Natural History which brought together paleoanthropologists, geologists, biochemists and geneticists alike. The main thrust of the conference was to resolve some of the controversy which still surrounded the study of early hominids. The results of the conference were published in 1985 (Delson, Ed.), and although consensus was certainly not reached, many different issues were explored.

Tobias (1985b) made an attempt to resolve one issue that he saw as causing significant problems in human paleontology. As a consequence of recent dramatic increases in the numbers of hominid fossils, detailed comparisons of single complexes or even traits were becoming possible, utilizing numerous representatives of said anatomical regions. Tobias lamented the fact that far-reaching phylogenetic interpretations were being made on these limited regions or traits, to the exclusion of the "total morphological pattern" of Le Gros Clark (1955). In order to demonstrate the pitfalls of such reduction, Tobias analyzed 7 distinct anatomical features to determine their ability to discriminate hominid taxa. What he found was that each morphological trait was capable of differentially separating out the species. By way of example, while the inion-opisthiocranion distance was capable of separating *Homo habilis* from *Australopithecus africanus* and *Australopithecus boisei*, as well as *Homo erectus*, it was incapable of separating *Australopithecus africanus* and *Australopithecus boisei* from *Homo erectus* (Tobias, 1985b:99). Similarly, the robusticity of the mandibular corpus was able to differentiate *Homo erectus* and *Homo habilis*, but failed to distinguish *Homo habilis* from *Australopithecus spp.*

Based on this, Tobias concluded that "if one were to rely on any one of these seven single traits to construct the pattern of systematic interrelationships and a phylogenetic scheme, one would obtain appreciably different results according to which trait one chose (Tobias, 1985b:99)." He criticized certain authors for their over-reliance on single traits or complexes, and called for "restraint in the drawing of systematic and phylogenetic conclusions from studies on a single trait, complex, or region of the body (Tobias, 1985b:95)." Rather, he advocated a return to the analysis of the "total morphological pattern" of Le Gros Clark (1955).

In the same volume, Olson looked at the morphological diversity of the Hadar hominids, and concluded that both 'robust' and 'gracile' elements were present, based on both basicranial and nasal morphology (Olson, 1985:114). He again indicated that the skull AL333-45 actually represented a member of the taxon *Paranthropus africanus* (see Olson, 1981, above for fuller discussion), and since the AL333 locality, colloquially called the 'first family', was proposed to have all been deposited at the same time, and in fact, to have possibly belonged to a single family unit, Olson felt that all these fossils were members of the species *Paranthropus africanus*. Also included in this hypodigm were the remains from Laetoli. *Paranthropus africanus* was referred to as the most primitive of the 'robust' clade, possessing numerous plesiomorphic characters (Olson, 1985:116).

Also present in the Hadar materials were much more 'gracile' elements, which Olson referred to *Homo aethiopicus*. This new taxon was named following Tobias (1980b), after he designated the Hadar fossils as *Australopithecus africanus aethiopicus*. Olson wished to transfer these fossils to the genus *Homo*, and the senior synonym became *aethiopicus* (Tobias, 1980a). Olson referred to AL288-1 (Lucy) as the lectotype (as Tobias had not named a holotype in 1980a), and certain of the other Hadar remains as paralectotypes. *Homo aethiopicus* was seen to be more primitive in the dentition than was *Homo africanus* (after Robinson, 1965; 1968; 1972), and was thus ancestral to it (Olson, 1985:116).

The existence of two taxa at Hadar, for Olson, meant that the site was sampling fossils from the period immediately succeeding the cladogenetic event that split the *Homo* and *Paranthropus* clades. In order to explain the many similarities found between the groups, Olson stated that "the many symplesiomorphic features in these two taxa suggest that the Hadar Formation samples a period very close in time to the origin of the *Paranthropus* and *Homo* lineages (Olson, 1985:117)." At some point around 3.5 Myr, the split occurred, producing the most primitive species of each independent lineage, *Homo aethiopicus* and *Paranthropus africanus*.

Kimbel et al. responded to Olson, claiming that "Olson's analysis of the Hadar/Laetoli sample is plagued by a persistent tendency to generalize from the morphology of a single individual to other specimens without providing any justification for doing so (Kimbel et al., 1985:135)." They also criticized him for his differential amounts of variation allowed into different taxa. In some cases (e.g., *Homo africanus*) he allowed widely divergent amounts of morphological variation, while for other taxa (e.g. *Homo* vs. *Paranthropus*) a small amount of difference was seen as separating two genera (Kimbel et al., 1985:135). Kimbel et al. thus performed a detailed comparison of the traits Olson used to distinguish his taxa, and concluded they had found numerous errors in his arguments which vitiated his phylogenetic scheme. Kimbel et al. were "unable to find any features of the *A. afarensis* mastoid region that convincingly demonstrate unique specializations shared with *A. robustus* and *A. boisei* (1985:136)." They found no evidence whatsoever of multiple hominid taxa in the Hadar samples.

A more complete cladistic analysis of the deciduous dentition of the australopithecines was performed to further elucidate their taxonomic relations (Grine, 1985a). The first conclusion reached was that the differences between the 'robust' and 'gracile' australopithecines was marked, with the former possessing a "substantial suite of synapomorphies that clearly distinguish them from the [latter] (Grine, 1985a:162)." It was also noted that "a variety of features also serve to differentiate among the Kromdraai, Swartkrans, and *A. boisei* samples (Grine, 1985a:162)." The Hadar and Laetoli samples were firmly placed within one single taxon as well, separate from *Australopithecus africanus*. Grine felt that *Australopithecus robustus* was ancestral to *Australopithecus crassidens*, the latter of which was in turn ancestral to *Australopithecus boisei* (1985a:164).

Further evidence for the position of *Australopithecus africanus* in the 'robust' lineage was provided in a discussion of certain aspects of its facial morphology (Rak, 1985a). Five morphological features bearing on the masticatory system of the australopithecines were selected for study, and the conclusion was reached that *Australopithecus africanus* was too derived, and *Homo habilis* too primitive, for the two to be closely related at all (Rak, 1985a:170). Since the direction of the specialization of *Australopithecus africanus* was in the 'robust' direction, it must be ancestral to these taxa alone.

The genus *Paranthropus* was, at the time, making a comeback of sorts. Clarke (1985) held that *Paranthropus* should be considered a valid genus separate from *Australopithecus*, and comprising *Paranthropus robustus* and *Paranthropus boisei*. He listed out a suite of 20 morphological features he felt separated the genus from *Australopithecus*, noting that ". . . it is easier to distinguish

Paranthropus from *Australopithecus africanus* than it is to distinguish *Australopithecus africanus* from early *Homo* (Clarke, 1985:172)." He further stressed that "if it is valid to place *Homo habilis* in a genus distinct from *Australopithecus*, it is far more justifiable to separate *Paranthropus* from *Australopithecus* (Clarke, 1985:172)." He did not, however, accept the phylogenetic scheme of White and Johanson (1979) which placed *Australopithecus africanus* into the 'robust' lineage. He felt there was no evidence which placed *Australopithecus africanus* outside of South Africa, and that there was no earlier form of *Paranthropus* morphologically intermediate between *Australopithecus africanus* and *Paranthropus*. As such, it was still possible that *Paranthropus* was not evolved from *Australopithecus africanus* (Clarke, 1985:176).

The phylogenetic scheme of Johanson and White (1979) and White et al. (1981) was met with some opposition at the *Ancestors* Conference. McHenry (1985) reanalyzed the evidence for the proposition that *Australopithecus africanus* was the ancestor of the 'robust' lineage, while *Australopithecus afarensis* gave rise to *Homo*. Based on a long list of derived features shared by *Australopithecus africanus*, *Australopithecus robustus + boisei*, and early *Homo*, but not by *Australopithecus afarensis*, McHenry concluded that *Australopithecus africanus* was the last common ancestor of both *Homo* and the 'robust' australopithecines. Although he accepted the existence of *Australopithecus afarensis* as a biologically valid taxon, he felt that "*A. africanus* immediately predates the appearance of *H. habilis* and *A. robustus+boisei*, and it shares with these species a suite of derived features that is absent in *A. afarensis* (McHenry, 1985:182)." *Australopithecus afarensis* gave rise to *Australopithecus africanus* which in turn gave rise to both *Australopithecus robustus* and *Australopithecus boisei*, as well as *Homo habilis*.

On the Diamond Jubilee of the discovery of the Taung skull in 1985, a symposium was held to mark the occasion. One of the papers given at the symposium took issue with the claims made in the previous years that the Taung skull was actually a member of the 'robust' clade (Grine, 1985b). Grine was able to conclude that "the dental characters possessed by the Taung specimen do not conform to the hypothesis that it represents a juvenile 'robust' australopithecine (Grine, 1985b:252)." There was no special relationship between the Taung skull and the 'robust' australopithecines, and the dental evidence showed it to be much closer to the fossils of Sterkfontein and Makapansgat, thus settling this small controversy which had quietly raged for a number of years.

It was again claimed that *Australopithecus africanus* belonged exclusively to the 'robust' lineage, and that comparison of the facial morphologies of *Australopithecus afarensis* and *Australopithecus africanus* showed that *Australopithecus afarensis* was the most generalized (Rak, 1985b:234). It was noted this time that some specimens of *Australopithecus africanus* did not fit this derived 'robust' image. These were claimed to be females of a highly sexually dimorphic population, or else they were young members of said population (Rak, 1985b:234). This was a preliminary conclusion, for which further work was required.

Johanson (1985) presented a list of 22 features which he felt were best able to consistently distinguish *Australopithecus afarensis* from *Australopithecus africanus*. Taken together, this constellation of features was held to be able to distinguish between the species of australopithecines, in the manner which Le Gros Clark (1955) had advocated. It was recognized that the phylogenetic interpretation of McHenry (1985) was plausible, but it was felt that the scheme erected by Johanson and White (1979) and by White et al. (1981) was the most parsimonious, and the most concordant with the available evidence (Johanson, 1985:209).

This view was contested, however. McHenry and Skelton (1985) were able to list out 42 traits that showed *Australopithecus africanus* was the last common ancestor of *Homo* and also of the 'robust' clade. They were also able to locate 19 traits that indicated *Australopithecus afarensis* was the last ancestor of *Homo*, and that *Australopithecus africanus* was derived in the direction of the 'robusts'. A resolution to this apparent conflict was postulated by McHenry and Skelton in the form of morphological complexes. If clusters of similar traits were lumped together into one complex (e.g., large tooth size, massive mandible, and large attachment areas for the muscles of mastication), the numbers of traits was much reduced. In this case, "a single genetic change could give a pleiotropic effect which would alter a great number of traits simultaneously (McHenry and Skelton, 1985:223)." By grouping numerous traits together, it was noted that only one functional complex of *Australopithecus* had to undergo an evolutionary reversal from *afarensis* to *africanus* to *Homo*. This further did not require the parallel evolution of 42 traits to evolve *afarensis* into *Homo* (McHenry and Skelton, 1985:225). Therefore it was concluded that *Australopithecus africanus* was the last common ancestor of *Homo* and the 'robust' lineage.

In a study of the facial morphology of the australopithecines, Rak (1985c) noted that the molarization of the premolars of *Australopithecus africanus* and later *Australopithecus robustus* lead to the formation of anterior pillars to support the increased occlusal load borne by these teeth (Rak, 1985:282). The subsequent retraction of the palate in *Australopithecus boisei* and *Homo* eliminated the need for such buttressing. Rak felt that facial morphology showed that *Australopithecus afarensis* was the last common ancestor of both the 'robust' australopithecines and *Homo*. The similarities between *Australopithecus africanus* and *Australopithecus robustus* indicated that *Australopithecus africanus* was already derived in the 'robust' direction, and was therefore excluded from the *Homo* lineage.

The cladistic methodology was once again applied to the field of human paleontology in 1986, in what has become the most comprehensive analysis of this sort to date (Skelton, McHenry, and Drawhorn, 1986). The conclusions reached by this study are still reverberating today, as a final resolution has still not been forthcoming. Essentially, this detailed cladistic analysis almost completely laid to rest all but two of the competing phylogenies that had been constructed to that date. The ultimate resolution of the controversy must await further fossil discoveries in the period between 2.0 and 4.0 Myr.

Skelton et al. utilized 69 traits which they felt were diagnostic of the hominids in general, and analyzed them with regard to their morphological polarity (in the strict cladistic sense). From this analysis they were able to obtain 12 distinct complexes of traits which aligned the species in differing ancestor-descendent relationships. Basically, morphological traits are polarized within a lineage, and shared derived states of the traits are used to imply a close recent common ancestor (at least closer than shared primitive traits). From these morphoclines (linear arrangements of traits from primitive to derived), phylogenies are constructed (branching diagrams which imply ancestor-descendent relationships).

Skelton et al. were able to conclude that ". . . the last common ancestor of *A. robustus/boisei* and *H. habilis* was derived relative to *A. africanus* (Skelton et al., 1986:30)." This is important as it implies that rather than a more primitive population giving rise to the two taxa (i.e. *Australopithecus afarensis*), a more derived population was required, contra Johanson and White (1979). Skelton et al. nonetheless concluded that the hypothesized last common ancestor would still fit within the species *Australopithecus africanus*. Although they accepted *Australopithecus afarensis* as a valid species, they did not feel that it was the last common ancestor, or that *Australopithecus africanus* was too derived on the direction of the 'robust' lineage to be ancestral to *Homo*.

Skelton et al. critically analyzed the 5 main competing phylogenies of the day, and demolished all but two of them. These final two, the phylogeny of Johanson and White (1979), and their own (which was essentially the same as that of Tobias (1980b) except that they held *Australopithecus afarensis* to be valid), are the two main competing hypotheses today, and the battle rages on between their proponents. Their conclusions provide an excellent summary of their results, and are worth quoting at length here.

> The presence of a number of derived traits that are shared by *A. africanus*, *A. robustus/boisei*, and *H. habilis* indicates that these three species are closely related and form an evolutionary group distinct from *A. afarensis* and any earlier species. Furthermore, the presence of derived traits that are shared only by *A. robustus/boisei* and *H. habilis* indicates that a population of hominids of the genus *Australopithecus* that closely resembled *A. africanus* but was even less primitive was probably the last common ancestor of the two. It can be regarded as unlikely that any species more ancient and/or primitive than *A. africanus* was the last ancestor of either the *Homo* lineage or the *A. robustus/boisei* lineage.
>
> The differences between our hypothesis and that of Tobias (1980b) are mainly a matter of taxonomy. The hypothesis of White, Johanson and Kimbel (1981) postulates the divergence of *Homo* from *A. afarensis* and cannot account for the shared derived traits that link *H. habilis* with *A. africanus* and *A. robustus/boisei*. Leakey's (1981) hypothesis postulates the divergence of *Homo* at an even earlier date and similarly fails to account for the aforementioned shared derived traits linking the later hominids. The hypotheses of Olson (1981) and Boaz (1983) derive *A. robustus/boisei* from *A. afarensis* or some even more ancient species and cannot account for the shared derived traits linking *A. robustus/boisei* with *A. africanus* and *H. habilis*. Taken together, these six phylogenies represent almost every logical way of arranging these species (Skelton, McHenry and Drawhorn, 1986:35).

An interesting sidenote is the fact that for the purpose of this cladistic analysis the authors were unable to separate the two 'robust' species, *Australopithecus robustus* and *Australopithecus boisei*, and were thus forced to consider them as a single morphological unit (Skelton, et al., 1986:22; note 4). Also, of the numerous replies which were made to the article, not one of them (even that of Kimbel, White and Johanson) challenged the taxonomic conclusion reached (Skelton and McHenry, 1986:363). The criticisms were all leveled at the cladistic methodology applied, or at least certain aspects of it as used by the original authors.

While this discussion was raging on, more exciting new fossil finds were being made at Lake Turkana in Kenya (Walker et al., 1986). Most notable was the nearly complete cranium designated KNM-WT17000, dated to approximately 2.5 Myr (Walker et al., 1986:519). The so-called "black skull " (owing to its manganese stained coloration) was thought to be a member of the East African species *Australopithecus boisei*, which would make it the earliest representative of this taxon. A suite of 40 morphological characters was gleaned from the analysis of Skelton et al. (1986), and compared with the new skull (the 40 traits were chosen as they represented those features present on the new skull). It was concluded that for most features the new skull most resembled *Australopithecus boisei* (Walker et al., 1986:521). Some differences were noted, but it was felt that these differences were either a result of its primitiveness or of normal intraspecific variation. Nonetheless, a cautionary note was added to the effect that it was possible that the differences might be sufficient to warrant a specific distinction, and as such, the appropriate name would be *Australopithecus aethiopicus*. This was named after *Paraustralopithecus aethiopicus* Arambourg and Coppens, which was based on a mandible found in 1967 at Omo in Ethiopia in a similar sedimentary basin of a similar age.

This find made the assertion of Rak that *Australopithecus robustus* was ancestral to *Australopithecus boisei* untenable, as this find was older than any other known 'robust' australopithecine (Walker et al., 1986:521). The position of *Australopithecus robustus* was suddenly in doubt, and it was hypothesized that it was derived from an ancestral species prior to 2.5 Myr, or that it was perhaps derived independently from *Australopithecus africanus* (Walker et al., 1986:521). This new find also challenged the view that *Australopithecus africanus* was the exclusive ancestor of the 'robust' lineage. There were many features of KNM-WT17000 which were clearly more primitive than *Australopithecus africanus*, and which allied it to *Australopithecus afarensis*, but it was still clear that KNM-WT17000 was a member of the 'robust' clade (Walker et al., 1986:521). A final tentative assertion was made that this new evidence might support the view of Olson that there were two taxa present at Hadar, one of which gave rise to *Australopithecus boisei*, and presumably, the Black Skull (Walker et al., 1986:522).

Commenting on the new fossil find, Delson (1986) was quick to point out that of the many traits listed by Walker et al., not all were diagnostic of *Australopithecus boisei*, and thus "the form represented by WT 17000 presents several features characterizing all robust forms but few specific to either *boisei* or *robustus* (Delson, 1986:497)." The implication of this was that it represented an ancestral form, not yet derived in the direction of one or the other 'robust' taxa, conceivably indicating the existence of a new species. Still, it was noted that "it is possible (although undemonstrated) that a form resembling *A. robustus* inhabited southern (or eastern) Africa between 3 and 2.5 Myr, giving rise to all post 2.5 Myr robust species including WT17000 (Delson, 1986:497)." Delson hypothesized that just over 3.0 Myr a cladogenic event split *Australopithecus afarensis* into *Australopithecus africanus* and an as yet unnamed species represented by KNM-WT17000. *Australopithecus africanus* lead to the *Homo* lineage, while the unnamed species lead to the 'robust' lineage.

The results of cladistic analyses are not always unequivocal, as noted by Wood and Chamberlain (1986). Based on an analysis of 39 cranial traits, they discovered that a number of different cladograms were produced, many of which were equally likely to be the correct one. They were able to conclude that *Australopithecus robustus* and *Australopithecus boisei* were quite distinct in morphology when compared to any other fossil hominid species, and as such, it was noted that the resurrection of the genus *Paranthropus* might be necessary (Wood and Chamberlain, 1986:236). They also felt there was strong evidence for the status of *Homo habilis* as a valid member of the genus *Homo*. As to the status of *Australopithecus africanus*, it was stated that "*A. africanus* shares character states with both the *Homo* and the 'robust' australopithecine clade" while "*A. afarensis* forms the sister group of the 'robust' australopithecine clade. . . (Wood and Chamberlain, 1986:237)." It would appear from this analysis that the evidence provided partial support for *Australopithecus africanus* as the last ancestor of the *Homo* lineage, and *Australopithecus afarensis* at the beginning of the 'robust' line.

A study of the fossils recovered from Omo in Ethiopia provided evidence contrary to the Johanson and White (1979) hypothesis (Hunt and Vitzthum, 1986). Based on a multivariate analysis of the Omo dental remains, Hunt and Vitzthum concluded that "since *A. africanus* is the only possible immediate ancestor of *H. habilis* yet discovered, and since the reversal required to fit *A. africanus* into the *Homo* lineage is not an unlikely event, *A. africanus* serves as the most likely known precursor to the *Homo* lineage (Hunt and Vitzthum, 1986:153)." They based this conclusion on the fact that they believed the Omo fossils belonged to *Australopithecus africanus*, and the presence of *Australopithecus africanus* at Omo made it much more likely that it was an ancestor of the *Homo* fossils found in the more recent levels of the same site. They concluded thus that there was no basis for removing *Australopithecus africanus* from the *Homo* lineage.

In 1986, new excavations were opened at the famed Olduvai Gorge in Tanzania under the leadership of Don Johanson (on hiatus from Hadar as a result of the unstable political situation in Ethiopia). These excavations were successful in procuring a new partially complete hominid skeleton which was referred to the species *Homo habilis* (Johanson, et al., 1987). It was hoped that this new find would help to alleviate some of the difficulties which were being noted for this particular taxon. Wood (1987) felt that it unfortunately had not. The taxon *Homo habilis* boasted within its hypodigm two 'varieties' which seemed irreconcilable. One was a larger brained and toothed version (including KNM-ER1470 and 1590), while the other was smaller and more gracile (including KNM-ER1813 and OH24). Some felt that the smaller version actually belonged to the genus *Australopithecus*, while others favored a new species of *Homo*. Wood alluded to the fact that the new skeleton might actually belong to *Australopithecus* rather than *Homo habilis*. The morphological heterogeneity of *Homo habilis* was unfortunately not mitigated by the new skeleton's discovery.

The validity of the genus *Paranthropus* was accepted as a given by some researchers, a trend which was becoming more common again. Benyon and Dean (1988) performed a study on the dental development patterns of the australopithecines, and were able to conclude that "this comparison of data from *Australopithecus* and *Paranthropus* supports the view that there are consistent major differences in dental development between *Australopithecus* and *Paranthropus* (Benyon and Dean, 1988:513)." Apparently these differences were enough to warrant a generic distinction.

Susman (1988) felt that the hand of *Paranthropus robustus* was adapted for a precision grasp, and therefore that it was capable of tool use. As such, an absence of tool use was not the cause of the 'robust' species' extinction, nor was it responsible for the later success of the *Homo* lineage (Susman, 1988:781). Susman and Brain (1988) further noticed that the hallucal morphology of *Paranthropus robustus* was essentially similar to the human condition, with a similar range of extension, differing only in the toe-off mechanism (Susman and Brain, 988:7).

When studying the morphometry of the australopithecine facial region, Bilsborough and Wood (1988) noted significant differences between the 'robust' and 'gracile' forms. Some of the more 'gracile' crania that had been assigned to *Homo habilis* (KNM-ER1813, KNM-ER1470, SK847) were noted to share certain features with *Australopithecus africanus*, or even the 'robust' species, but it was concluded that when combinations of features were compared, these skulls fell within the hominine pattern (though no specific designation was formally provided). *Homo erectus* showed a uniquely distinct pattern. Many of their measures were compared with the more non-metrical analyses of Rak and, though differences were noted (mainly with Rak's interpretations), an overall accord was reached with his work.

Recently opened explorations of the West side of Lake Turkana by Richard Leakey were turning up some truly remarkable finds. Many new crania attributed to *Australopithecus boisei* were turning up in wonderful states of preservation (Walker et al., 1986; Leakey and Walker, 1988). Many new mandibles were being found as well, and it was noted that the dubious taxonomic allocation of the Omo-1967-18 (type specimen for *Paraustralopithecus aethiopicus*) could finally be resolved; the mandible was in close conformity with those found at West Turkana, and therefore it was attributed to *Australopithecus boisei* (Leakey and Walker, 1988:22). Numerous other Omo fossils were also ascribed to *Australopithecus boisei* on the strength of the new fossil finds. Leakey and Walker questioned whether it would be valid to give different species names to geologically and chronologically widely spaced members of the same evolving lineage. Their question was directly aimed at the issue of KNM-WT17000, and whether it represented a new species, even though it was strongly considered to be directly ancestral to *Australopithecus boisei*. If it were to be considered a new species, then the name *aethiopicus* would be available. But again, caution was raised against naming different members of the same evolving lineage separately, as this would serve to obscure the true nature of the evolutionary relationships.

In 1988, another major conference was held in New York, this time dealing especially with the question of the 'robust' australopithecines and their true phyletic position amongst the hominids. Researchers from around the world were invited to participate, and do their part to help sort out the problems inherent in the study of these extinct relatives of ours. The conference was organized by Dr. Fred Grine of the State University of New York at Stony Brook.

Grine had long maintained a generic separation of *Paranthropus* from *Australopithecus*, and his first contribution to the conference echoed that conviction. Grine and Martin (1988) discovered that *Paranthropus* permanent molar enamel was relatively thicker than was that of *Homo* or *Australopithecus*, whereas the latter two shared similar thickness of their enamel. As for the various species of *Paranthropus*, it was noted that "differences among the teeth of *P. boisei*, *P, robustus*, and *P. crassidens* in the angles assumed by the striae over the cervical portion of the crown and in the configuration of the striae over the occlusal aspect, suggest that species level distinctions among these samples should be retained (Grine and Martin, 1988:39)."

Dean Falk pointed out that the discovery of KNM-WT17000 contradicted the theory that *Australopithecus africanus* was ancestral to the 'robust' clade of hominids. Rather, Falk indicated that, since both *Australopithecus afarensis* and *Australopithecus robustus/boisei* shared an enlarged occipital marginal sinus system to the exclusion of all other fossil hominids, it must be that the 'robusts' evolved out of a basal *Australopithecus* stock just prior to

Hadar, at around 4.0-4.5 Myr ago. In fact, it was claimed that ". . . the oldest fossil evidence of "robust" australopithecines is from Hadar, and some if not all of these specimens are depicted . . . as being members of the East African subspecies (race) of "robust" australopithecines (Falk, 1988:91)." KNM-WT17000 fit quite well into this new racial variety. Falk believed that the differences between the East and South African 'robusts' were due to subspecific, or racial, variation, and KNM-WT17000 was no exception.

William Jungers attempted to reconstruct the body size of both *Australopithecus* and *Paranthropus*. He found little evidence of major differences between the body sizes of any of the australopithecine groups, be they 'robust' or 'gracile' (Jungers, 1988:118). He also found sexual dimorphism to be marked amongst the groups. This conclusion on the size differences between the taxa was supported by another study using different methods, but essentially arriving at the same end result, namely that there was little difference in body size of any of the australopithecines (McHenry, 1988).

In a study of the morphological variation seen in the various species of the hominids, Kimbel and White noted that *Australopithecus afarensis* was seen to be quite homogeneous for dental metrical traits, in contrast to previous studies (Olson, 1981; 1985) which had claimed there were two taxa represented at Hadar. It was also shown that the pooled samples of Swartkrans and Kromdraai showed no excessive amounts of variation, and that there was no morphometric basis for separating *'Paranthropus' robustus* and *'Paranthropus' crassidens*. Evidence was also presented that the Sterkfontein site might actually represent two distinct species

(Kimbel and White, 1988:189). Oddly, they indicated at one point that the morphological variation seen at Sterkfontein should not be overlooked and simply subsumed within one species, but later contradicted this by saying that at Hadar such morphological variation should.

The newly found cranium, KNM-WT17000 presented some problems to Kimbel and White as well. They felt that "to subsume KNM-WT17000 in *A. boisei* would so elevate the level of morphological variation in this species that it could no longer be defined by the uniquely derived character states that distinguish it from *A. robustus*. Primarily for this reason, we regard KNM-WT17000 as a distinct species *A. aethiopicus* (Kimbel and White, 1988:189)." Exactly which "uniquely derived character states" they were referring to is difficult to determine since, in their own cladistic analysis of the australopithecines (White, Johanson and Kimbel, 1981; Kimbel et al., 1984), they were unable to consider the two 'robust' australopithecines as separate groups (implying that there were no uniquely derived character states separating *Australopithecus robustus* and *boisei*). Others as well could see no cladistic distinction between the two 'robust' species (Skelton, et al., 1986). It would thus appear that a new species was being named primarily to preserve a taxonomic distinction between two species that the authors could not previously separate out cladistically.

In his next contribution to the volume, Grine analyzed some new craniodental remains from Swartkrans, with an eye to comparisons with *Australopithecus robustus* as well as the other hominid species. In almost all of the dental measures there was overlap between *Australopithecus robustus* and "*Australopithecus crassidens*", though Grine was careful to note any distinctions between the two. The discovery of KNM-WT17000 negated the phylogenetic position of Johanson and White (1979), supported by Grine (1985). Grine considered the new skull to represent a new species of the genus *Paranthropus*, but was uncertain as to the phylogenetic interpretation this new skull would require of the genus *Paranthropus* (Grine, 1988a:242).

In an evaluation of the evolution of the 'robust' lineage, Walker and Leakey felt that it would be "unwise at present to cut up the lineage [*Australopithecus boisei*] into successive stages (1988:251)." This statement was referring to their earlier (Walker et al., 1986) suggestion that KNM-WT17000 might represent a new species. The new skull presented other problems as well, in that the evolutionary progression seen before from *Australopithecus robustus* to *boisei* as set out by Rak (1983) was no longer tenable. They concluded that "because of the *A. boisei* condition of the teeth, palate, face, and foramen magnum, we think that KNM-WT17000 was from a population after *A. robustus* had already diverged. Several features that are common to both "robust" species must have evolved in parallel (Walker and Leakey, 1988:256)." It was concluded that the 'robust' australopithecines might actually be polyphyletic, that they may have evolved many of their features in parallel after the divergence from a common ancestor which may have been KNM-WT17000 or earlier.

Kimbel, White and Johanson (1988) took issue with KNM-WT1700 next, attempting to place it within a revised phylogenetic scheme. Of the 40 traits that had been originally used to describe the specimen (Walker et al., 1986), the authors paired away 8 traits they felt to be either redundant or misleading. The remaining 32 traits were used to define a new species. The first step was to prove that the skull was not a member of *Australopithecus boisei*, which Kimbel et al. believed they were able to do. They again argued that to include KNM-WT17000 in *Australopithecus boisei* would require a revision of the definition of the 'robust' australopithecines to include both *Australopithecus boisei* and *robustus* since the two shared so many derived traits (Kimbel, et al., 1988:261). The possibility of this was precluded by recent studies which had purported to see specific differences between the two taxa (Howell, 1978; Rak, 1983; Kimbel et al., 1984; Grine, 1985; Wood and Chamberlain, 1986).

Since the skull appeared to be an amalgam of characters from different australopithecine taxa, a new species name was given to the find, *Australopithecus aethiopicus*. The trivial name *aethiopicus* was used because the authors felt that the original specimen of the defunct taxon *Paraustralopithecus aethiopicus*, Omo-1967-18, was seen to possess features which distinguished it from all other 'robust' mandibles (Kimbel, et al., 1988:263). KNM-WT17000 was assigned to the same species as Omo-1967-18, despite the lack of comparable material, since the authors held the Omo mandible to represent a valid species, and to attribute KNM-WT17000 to another species would imply the existence of two synchronic, sympatric, primitive 'robust' lineages. In essence, the authors felt they could distinguish a new species based on one single mandible (*aethiopicus* of 1967), and that the skull had simply to be assigned to this already existing species (even though no one had accepted the validity of *aethiopicus*).

Kimbel et al. (1988) contended that "the mosaic of primitive and derived characters exhibited by KNM-WT17000 indicates that *A. aethiopicus* is phylogenetically intermediate between *A. afarensis* and "robust" *Australopithecus* species. We contend that in morphology and known temporal range, *A. aethiopicus* could have been ancestral to *either* or *both A. robustus* and *A. boisei* (Kimbel, et al., 1988:263)." It is of interest to notice that a new species was named without a single characteristic defining it and no other species. This was truly a cladistic species, and there was no discussion whatsoever of its biological validity. A number of possible phylogenetic schemes were proposed to fit the new taxon, but the authors themselves were unable to come to any consensus on which was the most correct. As well, the position of *Australopithecus africanus* became even more problematic as it was considered to be ancestral to neither *Homo* nor the 'robusts'. It would seem that the oft called for swelling of the hominid fossil record had provided not illumination, but rather, confusion.

Wood noted that the case for a paraphyletic understanding of hominid evolution might be stronger than was previously believed. He felt that it might be possible that the two species of 'robust' *Australopithecus* might be descended from two separate ancestral stocks. He was willing to admit an extremely large amount of parallel evolution to take place by stating that the numerous cranial and dental features shared by the two taxa could have developed independently (Wood, 1988:278).

Clarke (1988) was able to detect two distinct species in the Sterkfontein materials, something no one else had considered. He saw "a small toothed hominid with thick supraorbital margin and prominent nasal skeleton" and "a large toothed hominid with thin supraorbital margin and flat or concave nasal skeleton (Clarke, 1988:289)." He ruled out sexual dimorphism, individual variation and change through time as causes, citing different species as the most plausible explanation for the noted differences. He felt that the undetermined species was tending towards a 'robust' condition, and that it represented *Paranthropus*.

Tobias presented a cladistic argument supporting the hypothesis of Skelton et al. (1986) which showed a minimum of 42 traits shared by *Homo habilis*, *Australopithecus robustus* and *Australopithecus boisei* as contrasted to their condition in *Australopithecus africanus*. These were presented as strong support of Skelton et al. (1986) that *Australopithecus africanus* was the last common ancestor of the two lineages. The parallel evolution of such a large list of traits did not at all seem likely (Tobias, 1988:305).

In a rebuttal of Rak (1985c), McKee (1989) noted that the construction of phylogenies cannot be based on singular morphological traits. Rather, entire morphological patterns must be considered. As evidence, McKee noted that the anterior pillars held by Rak to be so phylogenetically important in specific distinctions of *Australopithecus africanus* and *Australopithecus robustus* were in fact widespread in hominids, even being found in *Homo sapiens* (McKee, 1989:8). This contradicted part of Rak's argument that saw

Australopithecus africanus as uniquely derived in the direction of *Australopithecus robustus*.

In a criticism of the cladistic approaches which were becoming increasingly popular, Tobias (1989a) noted that errors of interpretation happened on occasion, and that these errors were further compounded by different researchers re-employing these incorrectly interpreted traits in subsequent analyses. He also felt that insufficient sample sizes biased cladistic studies by not revealing the full range of morphological variation allowed by a taxon. The chronological and geographical distances between fossil samples must be accounted for as well, lest further mistakes are made. Tobias also claimed that the Taung skull might represent the '*derived Australopithecus africanus*' population sought for by Skelton et al. (1986). He also noted that he ". . . does not yet see sufficient evidence to justify the creation of a new species, *A. aethíopicus* to accommodate KNM-WT17000, KNM-WT16005, and Omo-1967-18 (Tobias, 1989a:125)."

It was finally in 1987 that Tobias was able to exclaim with confidence that *Homo habilis* was a widely, if not universally, accepted taxon of hominid fossils (Tobias, 1989b:153). In spite of the criticisms and opposition that the species had received since its naming in 1964 (Leakey, et al., 1964), the Round Table of the Second International Congress of Human Paleontology (1987) dealing particularly with *Homo habilis* helped to confirm its existence. Tobias felt that the species was an example of a premature discovery, one whose impact and relevance would not be accepted and understood for years after its initial proposal (Tobias, 1989b:152). He did, nonetheless, note a number of problems that were still inherent to the species, notably the possibility that there might be two taxa represented in the hypodigm (exemplified by the difference between KNM-ER1470 and KNM-ER1813), and the fact that the hypodigm itself was controversial, with different researchers placing different specimens therein (Tobias, 1989c:143).

In a study of the stature of early hominids, McHenry (1991a) was able to estimate body size based on reconstructions of femoral lengths. He noted strong sexual dimorphism in the skeletons of both *Australopithecus afarensis* and *Homo habilis*, but less dimorphism in *Australopithecus africanus*, *Australopithecus robustus*, *Australopithecus boisei*, and *Homo erectus*. He raised the possibility that the extreme dimorphism of *Homo habilis* might actually be indicative of the fact that there are two taxa represented (McHenry, 1991a:156). It was also noted that the presumed increase in stature during human evolution might not in fact be true, as certain of the hominids from 1.7-2.0 Myr were of typical human height. In spite of these estimates, it was still noted that individual isolated postcranial remains could not be allocated to a species with a great degree of certainty owing to the similarity between taxa noted for many of the postcranial remains (McHenry, 1992:429).

In a similar study, McHenry (1991b) also estimated the body weight sexual dimorphism of *Australopithecus afarensis*. He discovered that the sexual dimorphism in body size had previously been overestimated, and that in fact, *Australopithecus afarensis* exhibited a moderate level of body size dimorphism (McHenry, 1991b:30). The pattern was seen to be significantly greater than modern humans and chimpanzees, but was lower than gorillas and orang-utans. The conclusion was reached that this moderate level of dimorphism argued against the view that there might be two taxa represented at Hadar.

The controversial new skull, KNM-WT17000 continued to exhibit new features that were thought to be diagnostic of it. It was noted that the squamosal suture of the skull was quite different from that seen in *Australopithecus boisei* (Rak and Kimbel, 1991:4). Although the authors admitted this might simply represent individual variation, it was their belief that future discoveries would corroborate their claim. This was further proof that the skull was in fact different from *Australopithecus boisei*, and that it represented a new taxon.

Another cladistic analysis was performed on the fossil hominids, this time including more taxa and more traits than had previously been utilized (Wood, 1992a). It was noted that the skull KNM-WT17000 shared a number of traits with *Australopithecus boisei*, and that they were very closely related (though Wood still asserted that KNM-WT17000 was distinct). Wood referred to the find as *Paranthropus aff. P. boisei*, which essentially removed it from *Australopithecus aethiopicus*. The original namer of the Omo-1967-18 mandible, for which *aethiopicus* was erected, also referred his mandible to *Australopithecus boisei* (Coppens, 1980). This removed said mandible from *Australopithecus aethiopicus* as well, and left the taxon empty. As such, since the taxon was an empty nomen, with no referred materials, it should be formally sunk.

Based on an assumption of polyphyly for the 'robust' australopithecines, Wood noted that *Australopithecus afarensis* was not primitive enough to be the last common ancestor of both the 'robusts' and *Australopithecus africanus* (Wood, 1992a:353). In the discussion of the assumption that the 'robust' australopithecines were polyphyletic, no mention was made of the large number of unique derived traits shared by the two 'robust' taxa, or the phenomenal amount of parallel evolution required for this assumption to be met. When polyphyly was not assumed, the two 'robust' taxa were associated again as sister taxa (Wood, 1992a:357). It was also noted that the majority of cladistic studies done in the past linked the two as sister taxa, indicating that they shared exclusively a common ancestor (Wood, 1992a:356). The simple fact that *Paranthropus robustus* and *Paranthropus boisei* were associated as sister taxa was used as evidence that the genus *Paranthropus* was in fact valid [ignoring the fact that the two had, since 1954, always been considered sister taxa, and that previous discussions of the facial and dental features discussed by Wood had not separated the two generically (Rak, 1983; Tobias, 1967)]

The taxon *Paranthropus crassidens* was apparently considered a valid one by Wood, although its hypodigm was subsumed within *Paranthropus robustus*, as the differences between the two were mainly dental, and quite difficult to detect (Wood, 1992a:356).

A new species of the genus *Homo* was included in the study, *Homo rudolfensis*. It was believed that the amount of intraspecific variation in the taxon *Homo habilis* was great enough to warrant the erection of yet another new hominid taxon (Wood, 1992a:359) to accommodate the larger of the fossils (e.g., KNM-ER1470). *Homo habilis* and *Homo rudolfensis* were listed as sister taxa, though little information was given as to why the two were considered different species, other than a vague notion of "higher levels of variation than are found in suitable living and fossil analogues (Wood, 1992a:358)." It was also noted that a polyphyletic view of *Homo* was only slightly less parsimonious than a monophyletic one, with *Homo rudolfensis* sharing numerous synapomorphies with *Paranthropus* (even though this would negate the idea of *rudolfensis* belonging to the genus *Homo*).

And finally, still yet another new taxon was accepted as biologically valid, this time *Homo ergaster*, which was considered distinct from *Homo erectus* based on a few traits and no discussion of validity (Wood, 1992a:360).

In all this study was extremely confused and confusing, utilizing numerous new hominid taxa with no support for their actual biological validity. An almost ludicrous amount of taxonomic splitting was accepted as perfectly sound, and the resulting phylogenetic tree provided more bewilderment than illumination. It would appear that in the rush to accept cladistic and statistical species as important and useful, the concept of reproductively isolated populations of living, breathing, interbreeding animals as constituents of species has been misplaced.

In another article, Wood (1992b) did outline some of his reasons for accepting two new species of the genus *Homo*, though the reasoning was not exhaustive. Both species had been named by others, and Wood left the formal descriptions to them. Though these species of the genus *Homo* are beyond the scope of the present study, they nonetheless serve to illustrate the significant amounts of taxonomic overabundance that can occur when extreme reliance is placed on one single method of phylogenetic interpretation. The true meaning of species gets lost in the discussions of minute differences in small morphological features, and typological classifications take the forefront.

The year 1993 marked the announcement of the first new hominid site discovered in South Africa since 1948. The site of Gladysvale, in the Transvaal region, is located close to both Sterkfontein, Swartkrans, and Kromdraai, and has been dated approximately between 1.7 and 2.5 Myr (Berger et al., 1993:107). The newly discovered fossil teeth were attributed to *Australopithecus cf. africanus*, and it was hoped that future discoveries would clarify the phyletic position of these specimens.

The early hominid sites in East Turkana in Kenya were also continually producing new hominid fossil remains. Another partially complete *Australopithecus boisei* cranium was recovered from the site, dated to approximately 1.9 Myr (Brown et al., 1993:137). The new skull, KNM-ER23000 was quite similar to other *Australopithecus boisei* specimens from East Africa, including KNM-ER406, KNM-ER13750 and OH5. It provided a view of the variation of the species *Australopithecus boisei*, but also provided a closer link between said species and *Australopithecus robustus*. It was noted that "in the case of supraorbital torus and zygomatic arch configuration, Rak (1983) suggested that these features differed from those found in *A. robustus* in a characteristic way. This new specimen shows that the issue is more complex. If a difference in toral and arch morphology is to be found which differentiates the two species, it will be statistical rather than discrete (Brown et al., 1993:156)."

In a study of the sub-nasal morphology of the early hominids, McCollum et al. (1993) noted that the 'robust' taxa shared a distinct pattern, and that "the identification of this consistent morphological pattern within the 'robust' taxa is further evidence in support of their generic distinction (McCollum et al., 1993:110)." They were unable, however, to "identify a consistent subnasal pattern within the early *Homo* sample [which] may be further evidence for the presence of more than one species in this sample (McCollum et al., 1993:110)." The authors indicated that this analysis had vindicated the claims of Robinson (1953; 1954) of the taxonomic significance of this region.

In 1994 a nearly complete skull of the species *Australopithecus afarensis* was finally found, and it would serve to answer a number of questions regarding the cranial morphology of this taxon (Kimbel et al., 1994). The new fossils recovered supported the taxonomic unity of the species, indicating only one species in the Hadar remains (Kimbel et al., 1994:451). They also showed a significant amount of morphological stasis through 0.9 Myr.

Commenting on the new Hadar fossils, Aiello (1994) noted that the size differences between the extremely large new finds and those of Lucy were quite marked. It seemed difficult to accommodate them both within the same taxon. Nonetheless, the high degree of sexual dimorphism known to be present in the early hominids was invoked to explain away this apparent difficulty. It was further postulated that it was *Australopithecus afarensis* that made the famous footprints at Laetoli, and the new fossils tended to support the view that *Australopithecus afarensis* walked bipedally erect, but still retained the ability to climb in the trees (Aiello, 1994:399).

The final stop in our taxonomic saga came in 1994, when White, Suwa and Asfaw announced their new species *Australopithecus ramidus.* A new hominid fossil site at Aramis, in Ethiopia, had been discovered which dated to around 4.4 Myr (White et al., 1994:306). The morphology of the new specimens appeared so primitive that comparisons with African apes were necessary, and it was presumed that these fossils represented a stage immediately post dating the human-chimpanzee split. It was noted that further recoveries from the site might necessitate a reassessment at the generic and familial levels, though the fossils were definitely attributed to the hominid clade (White et al., 1994:312).

Commenting on the new species, Wood (1994) indicated that the fossils were morphologically quite distinct from *Australopithecus afarensis*. The differences were mostly dental, with many of these represented by deciduous dentition. Wood felt that the fit into *Australopithecus* was uncomfortable, as it was within *Pan* as well. He stated "my own personal prejudice is that, even on the present evidence, the differences between the Aramis species and *A. afarensis* are more profound, and are more likely to reflect the sort of grade distinction that is most usefully reflected in generic distinctions than are the differences between, say, *A. afarensis* and *A. africanus* (Wood, 1994:281)." He presumably was afforded a close examination of the fossils before he erected his new genus.

The final decision was delivered in 1995, when White, Suwa, and Asfaw transferred the Aramis remains from *Australopithecus* to a new genus, *Ardipithecus*. Neither detail nor justification was given for the erection of a new genus, nor were any further morphologically distinctive features noted. The authors apparently decided that they had a new genus on their hands, and presumably, a phylogenetic interpretation will be forthcoming.

It is here that our odyssey through the taxonomy of the australopithecines ends. The majors features extracted from each relevant work have been listed out below in chapter 3, and the actual analysis of these features will be undertaken in chapters 4 and 5.

Table 1. Important Events in Australopithecine Paleontology

Raymond Dart, 1925	*Australopithecus africanus* named
Robert Broom, 1936	*Australopithecus transvaalensis* named
Robert Broom, 1938	*Plesianthropus* named to house *transvaalensis*
Robert Broom, 1938	*Paranthropus robustus* named
Raymond Dart, 1948	*Australopithecus prometheus* named
Robert Broom, 1949	*Paranthropus crassidens* named
John Robinson, 1954	Australopithecine taxonomy re-written
W. Le Gros Clark, 1955	Genus *Australopithecus* and species defined
Louis Leakey, 1959	*Zinjanthropus boisei* named
Phillip Tobias, 1967	all australopithecine taxa officially defined
Don Johanson, 1978	*Australopithecus afarensis* named
Kimbel et al., 1988	*Australopithecus aethiopicus* presented
White et al., 1994	*Australopithecus ramidus* named
White et al., 1995	*Ardipithecus* named to house *ramidus*

Chapter 3 - Traits Selected for Analysis

3.1 Trait Selection

The traits selected for this thesis were taken directly from the literature of the field of paleoanthropology. A comprehensive review of all relevant literature from 1925 until the present was performed (chapter 2), and all traits that were indicated as being diagnostic for a given genus or species were recorded for analysis. Only those traits firmly pronounced as being indicative of a species were accepted. What this means is that the descriptions of various fossils were not employed unless it was stated by the author that a particular trait identified a species. Many volumes have been published giving detailed anatomical descriptions of the hominid fossils, but not every morphological feature was identified as belonging to one species only. Therefore, only those traits used to argue pro or con for any species were employed here.

The genera and species of the australopithecines have been periodically redefined, and occasionally certain of these genera and species were sunk in favor of other, already extant taxa. This has provided not a little confusion in the past, as well as for this thesis. Traits that were originally identified as being indicative of a certain species may have been dropped in the process, while other new ones were added. The format this thesis will follow will be to utilize mainly the primary sources that dealt particularly with the taxonomy of the australopithecines. Those works which were produced in an effort to delineate the morphological characteristics that defined the species will be perused to glean all the relevant character traits for each species.

Each individual taxon will be analyzed with respect to the various traits that were used initially to define it, as well as any arguments that may have been made to either support or deny its validity. An assessment will then be made (in the following chapters) of each taxon. Certain taxa have been sunk in the past in favor of other taxa, and some of the traits have been transferred to the new taxon as diagnostic of that new taxon. The new taxon will be analyzed with respect to all the traits that define it subsequent to any taxonomic revisions. An example will serve to clarify this. When *Zinjanthropus boisei* was initially named in 1959, it met with stiff resistance. The genus name *Zinjanthropus* was eventually sunk in favor of *Australopithecus*, but the specific status of *boisei* was maintained. Therefore, the traits that were used to maintain that specific distinction will be transferred to *Australopithecus boisei*. Although *Zinjanthropus* failed as a genus, *boisei* was upheld as a species, based on the original description offered in 1959, and on the later work of Tobias (1967b). These traits still define the species *boisei*.

It has been noted that, for the most part, discussions of traits used to discriminate hominid fossil species are normally limited to the original descriptions given of the various species. The original namers listed what they felt to be important features, and subsequent discussions tended to focus on analyses of these diagnostic traits. Occasionally, researchers have provided independent diagnoses of the various hominid fossil species throughout the years, and it is these, as well as the original namings, that will be dealt with for the most part (though other relevant discussions of taxonomy, phylogenetics and systematics will certainly not be eliminated). Therefore, this thesis will deal mainly with those works that deal expressly with taxonomic issues and character traits.

For the purpose of this study, diagnoses of species and diagnoses of genera will be kept separate. The two taxonomic categories are quite distinct, and various researchers have at times analyzed the two categories separately. Many of the past discussions have revolved around the validity of genera versus species. Therefore, there are enough discussions of those morphological features which are believed to be capable of separating genera to allow for a treatment of the generic status as well as the specific status of the australopithecines. In this study I will first discuss the species of australopithecines without overly too much concern for their generic status, and then discuss the genera that house the various species. For example, the specific status of *Australopithecus boisei* will be discussed apart from its generic status first, and then the reasoning behind its placement in either *Zinjanthropus*, *Paranthropus*, or *Australopithecus* will be discussed.

One further point must be noted here. When the field of paleoanthropology was still in its infancy, a great deal of the research being done was focused on the distinction between the hominid fossils and extant primate species, mainly the chimpanzee and gorilla. Until the exposure of the Piltdown forgery, men such as Dart, Broom, and Le Gros Clark were very careful in their work to specify exactly those traits which allied the australopithecines to humans and separated them from the apes. It is assumed that all readers of this work will have already accepted the fact that humans and apes have a very close phylogenetic relationship, and therefore traits distinguishing australopithecines from apes are not in need of review. These traits are of no significance to this study, and have been left out of the analyses. The only traits which will be studied are those which distinguish the australopithecines from one another, or which have at least been claimed to be able to do such.

A significant amount of anatomical morphological terminology will be used in this thesis, some of which may be unfamiliar. Readers are referred to Tim Whites excellently detailed and illustrated textbook, *Human Osteology*. For illustrations of the australopithecine morphology, please refer to *The Australopitheine Face* by Yoel Rak.

All taxa will be discussed in the order in which they were initially named, from 1925 onward.

3.2 The Species of the Australopithecines

Brief mention will be made of the source of the traits, and then the lists of characteristic features will be presented exactly as originally described by the various authors.

3.2.1 *Australopithecus africanus* Dart

When Dart described his new species in 1925, he based it on these morphological traits:

- enhanced relationship of cerebral length to facial length to accommodate larger brain (not bone)

- orbits are circular, not sub rectangular
- dentition humanoid, not anthropoid
- diastema between canines and lateral incisors of the upper jaw
- no diastema between premolars and canines on lower jaw
- incisors do not project forward
- jaw has parabolic arrangement
- short and slender mandibular ramus, composed of more massive bone than for human
- no simian shelf
- forward situated foramen magnum, gives head-balancing index similar to human (bipedal trait)
- lack massive canines
- cranium markedly dolichocephalic and leptoprosopic
- glabella tolerably pronounced, but supra-orbital ridges absent (on Taung skull)
- facial prognathism relatively slight
- nasal bones are not prolonged below the level of the lower orbital margins, completely fused in the lower half
- nasal aperture small and just wider than it is high
- glabella-inion length shorter than chimps and gorillas
- no nasal spine
- basi-prosthion measurement, plus basi-inion measurement: head balancing index, shows erectness of stature; basi-inion/basi-prosthion
- short length of nasal bones

In 1946, Broom gave a rediagnosis of the South African fossil hominid species. He essentially reiterated the morphological traits Dart had originally pointed out, but he also added a few traits of his own:

- lower border of the nasals a little above the general level of lower orbital margins
- well developed anterior fovea on first lower permanent molar, but no posterior fovea

In 1954 Robinson performed a much needed reanalysis of the South African fossil taxonomy wherein he formally sank

Plesianthropus and attributed all of its materials to the genus *Australopithecus*, relying on subspecific distinctions to separate the different sites. For *Australopithecus*, he saw the following features as being highly indicative of the species *africanus*. Since he recognized only one species, Robinson stated that the traits which defined the species also defined the genus, therefore, these are the same traits as used in the generic diagnosis:

- lower deciduous 1st molar incompletely molarized, protoconid most strongly developed cusp (incl. anterior accessory cusplet) with large sloping buccal surface
- vomer does not insert directly against back of anterior nasal spine
- P3 usually having a single buccal root
- canines large with mandibular canine strongly asymmetrical and lingual ridge present, normally strongly developed
- skull narrow, forehead present, supraorbital torus not strongly developed

He also recognized a number of subspecies, whose function it became to account for the variation seen at the different australopithecine sites:

Australopithecus africanus africanus

- tuberculum sextum present on M1
- deciduous canine without mesial cusplet

Australopithecus africanus transvaalensis

- M1 without tuberculum sextum
- protostylid common and may be large
- deciduous canine with mesial cusplet

The australopithecine taxa were again rediagnosed in 1967 by Tobias, and he defined *Australopithecus africanus* ,as being delineated by these features:

- gracile, lighter construction of the cranium
- calvaria hafted to facial skeleton at high level, giving forehead and high supra-orbital index
- ectocranial superstructures and pneumatisation not as marked as in other species
- sagittal crest commonly absent though probably present in some individuals
- nuchal crest not present, but slight to moderate occipital torus commonly present
- bony face of moderate height and varying from flat and orthognathous to markedly prognathous
- nasal region slightly elevated from facial plane
- ramus of mandible of moderate height and sloping somewhat backward
- jaws moderate in size with lesser development of zygomatic arch, pterygoid plate, temporal crest and fossa
- palate of more or less even depth, shelving steeply in front of the incisive foramen
- premolars and molars of moderate size and not so markedly expanded buccolingually
- M3 smaller than M2 in mesiodistal diameters, but equal in buccolingual diameters
- mandibular canine larger than in other species, and more in harmony with the postcanine teeth
- degree of moralization of lower first deciduous molar less complete
- cingulum remnants or derivatives present on all maxillary molars, weak on buccal, pronounced on lingual
- sockets of anterior teeth arranged in a moderate to marked curve

The final major work in australopithecine taxonomy to be looked at is that of Rak, published in 1983, and called *The Australopithecine Face*. In this work Rak analyzed the facial region of all known hominid fossils, and was able to point out a number of features that he felt were diagnostic of each of the australopithecines. For *Australopithecus africanus*, he saw these features as being capable of separating it from all other species:

- anterior pillars present
- maxillary furrow present (modified form of the canine fossa)
- zygomatic prominence present (pronounced bulbous corner on the zygomatic arch)
- wide flaring of the zygomatic arch; measure max. bi-orbital width, max. width of zygomatics, and divide the two to get an index; much larger in *Australopithecus*
- supra-orbital region in *A. africanus* is not separated from the squama by supratoral sulcus
- supraorbital tori do not descend medially, but merge to a prominent glabella
- nasal bones widen inferiorly and are usually flat on the same (coronal) plane
- nasal bones sharp superior, blunt inferior
- rounded lateral margins of the pyriform aperture, therefore not distinctly demarcated like *Homo*
- distinct ridgelike sill separates the nasoalveolar clivus from the nasal cavity, at the inferior margin of the nasal opening
- anterior pillars and nasoalveolar clivus stretched between them form a nasoalveolar triangular frame (elevated from the rest of the face, unlike *Homo*)
- zygomaticoalveolar crest - inferior margins of the zygomatic process; angles down from top to dental arcade V (horizontal. in apes and humans)
- facial height index I - measure from supraglabellar region to alveolar plane divided by bi-orbital breadth
- facial height index II - measure from supraglabellar region to alveolar plane divided by maximum bizygomatic breadth
- bizygomatic breadth index at plane of orbits
- bizygomatic breadth index - maximum: (ZY-ZY)
- postorbital constriction index - breadth
- biorbital breadth index
- facial height - nasion to alveolar (the usual measure replaced by Rak with supraglabellar to alveolar - used to calculate indices)
- palate relatively deep

3.2.2 *Australopithecus (Plesianthropus)transvaalensis* Broom

The next species of hominid to be named, *Australopithecus transvaalensis* was at first considered by its namer Broom to be congeneric with *Australopithecus africanus*. He subsequently placed it within its own genus, but the generic status of *Plesianthropus* will be looked at below. For now, we will discuss the following traits, which Broom believed separated *transvaalensis* from *africanus*:

- cranial capacity (of specimen) 600cc.
- moderately developed brow ridges
- fairly large frontal sinuses
- canine relatively small
- 1st molar moderately large
- 2nd molar exceptionally large with four large cusps and well marked posterior fovea
- 3rd molar with three well developed cusps and small hypocone due to large fovea - wrinkled crown

3.2.3 *Australopithecus (Paranthropus) robustus* Broom

In 1938, Broom discovered a third hominid species, which he again felt warranted a generic distinction from *Australopithecus*. Again, the generic status of *Paranthropus* will be discussed below, as well as the reasons for and against its validity. It (*robustus*) was initially based on these morphological traits:

- cranial capacity approx. 600 cc (Kromdraai skull)
- relatively small canines
- tympanic bone situated mainly below the posterior glenoid process
- occipital condyle in practically the same plane as the external auditory meatus

- face remarkably flat
- bony ridge runs down from inner border of the large infraorbital foramen
- 2nd premolar 50% larger than Sterkfontein
- incisors relatively small; laterals scarcely larger than centrals
- palate relatively short and small, anteriorly narrowed
- premolars without marked cusps, and with rounded crowns, twice as large as man
- 2nd premolar differs very markedly from that of *Plesianthropus transvaalensis*, and we may thus confidently place the new skull in a new genus and species

In the same paper wherein Robinson sank many of the australopithecine genera (1954), he also rediagnosed the different species. Regarding *robustus* (for which he maintained a generic distinction in *Paranthropus*), Robinson saw these features as defining the species, and as separating out the subspecies:

Paranthropus robustus

- crown of P4 appreciably larger than that of P3
- root of P4 double

Paranthropus robustus robustus

- deciduous maxillary canine symmetrical with very small distal cusplet
- deciduous lower 1st molar with no mesiobuccal cusplet anterior to anterior fovea

Paranthropus robustus crassidens

- deciduous lower canine markedly asymmetrical with distal cusp well developed
- deciduous lower 1st molar with mesiobuccal cusplet

Again in 1967 the species *robustus* was rediagnosed by Tobias, and regarded as being defined by the following:

- more robust, heavier construction of the cranium
- calvaria hafted to the facial skeleton at low level, with absent forehead & low supra-orbital index
- well developed ectocranial structures and degree of pneumatisation (more than *africanus*, less than *boisei)*
- moderate or marked supra-orbital torus with no twist between the medial and lateral components
- sagittal crest normally present
- small nuchal crest commonly present
- bony face of low to moderate height, and flat or orthognathous
- nose set in central facial hollow
- ramus of mandible very high and vertical
- jaws large and robust with strong development of zygomatic arch, lateral pterygoid plate, temporal crest and temporal fossa
- palate deeper posteriorly than anteriorly, shelving gradually from the molar region forwards
- premolars and molars of very large size
- M3 commonly larger than M2 in both buccolingual and mesiodistal diameters
- mandibular canine absolutely and relatively small and not in harmony with postcanine teeth
- degree of molarization of lower first deciduous molar more complete
- cingulum remnants only weakly represented on lingual face and absent on buccal face of maxillary molars
- sockets of anterior teeth arranged in a low to moderate curve

Previous to this diagnosis, *Paranthropus* had been sunk as a valid genus. The reasons for this will be discussed below.

Rak also dealt with the morphology of the facial region of this species, and listed these traits as specific to *Australopithecus robustus*:

- zygomaticomaxillary step (sort of a second anterior pillar, just under the orbits)
- zygomaticomaxillary fossa (groove crossing the zygomaticomaxillary step in the lower third in all individuals)
- anterior pillars; the width and degree of upward extension of the anterior pillar toward the frontal bone appear larger in *robustus* than *africanus*
- anterior pillar's elevation above the bone surface next to it (the zygomatic process) in *robustus* modest compared to *africanus*
- maxillary trigon - gutterlike triangular shape to infraorbital region between anterior pillar and zygomaticomaxillary step
- infraorbital foramen appears very low on the anterior surface of the maxilla close to the inferomedial corner of the trigon, contrasted to *africanus'* more normal position
- maxillary fossula - elongated fovea found near alveolar end of anterior pillar
- subforamen divide - bone table of the maxillary trigon surface completely separates the infraorbital foramen and the maxillary fossula
- zygomatic prominence - greater height of zygomatic in robustus leads to an elongated zygomatic prominence over *africanus* that extends downwards from the inferior orbital margins
- inferior margins of orbits - lateral part extremely blunt and wide anteroposteriorly; they protrude as a shelf beyond the coronal plane of the superior margins of the orbit
- inferior margins of orbits - medial part extremely sharp, and the transition between blunt (lateral) and the thin sections is abrupt
- zygomaticomaxillary step appears to continue topographically into medial thin segment of orbital margins
- this change in the inferior margin of orbits can be seen in humans and gorillas, but not chimps
- delicate supraorbital torus, arched orbits; torus follows shape of superior margins of orbits, and is continuously uniform
- supraglabellar fossa below the level of the torus between the orbits
- considerable post-orbital constriction, with no sign of a supratoral sulcus (same as *africanus*)
- interorbital/biorbital index calculated
- glabella and nasion appear to be either overlapping or in great proximity

- sharp inferior edges of the nasals merge inferolaterally into the blunt lateral margins of the pyriform aperture and become obliterated (like in *africanus*)
- inferior margins of the pyriform aperture lack the sharp sill that separates the nasoalveolar clivus from the floor of the nasal cavity in *africanus*; the transition thus is rather smooth
- nasoalveolar gutter - lower part of clivus found on same coronal plane as anterior pillars; closer to pyriform, more sunken relative to pillars
- clivus mostly flat; nasoalveolar clivus and the two pillars bordering it (forming the nasoalveolar gutter) are consistent morphological character
- face appears to have upwardly tapering contour, much like *africanus*; extends from inferior part of root of zygomatic arch up
- frontal process of zygomatic slopes downward and forward, contra to apes and humans
- zygomatic prominence constitutes lateral profile, instead of anterior pillars in *africanus*, in the upper face
- post orbital constriction very pronounced
- facial height - measure from supraglabellar region to alveolar plane
- bizygomatic breadth at plane of orbits
- bizygomatic breadth - maximum: (ZY-ZY)
- postorbital constriction - breadth
- biorbital breadth
- facial height - nasion to alveolar (the usual measure replaced by Rak with supraglabellar to alveolar)
- sagittal crest formed as result of union of the two inferior temporal lines
- frontal trigon - that part of the frontal bone surface not covered by the temporal muscles; shallow basin like appearance in *robustus*
- only slight anterior tapering seen in the post canine dentition, almost parallel
- the sockets for the canines and the incisors are usually on the same line as the mesial face of P3 for the species
- palate becomes shallower as it progresses anteriorly

3.2.4 *Australopithecus prometheus* Dart

Dart named this species in 1948 to accommodate the fossils found at the site of Makapansgat:

- thickened bone of skull - based on the occipital bone of one individual
- paedomorphic torus occipitalis
- occipital bone with its expanded planum occipitale, sutura mendosa, and parieto-occipital system of sutural ossifications
- low lying inion and elevated opisthocranion and reduced planum nuchale
- retardation of sutural obliteration and the concomitant expansion of the tempero-parieto-occipital association areas of the brain
- also discusses the importance of the "evidence" of fire use and ODK hunting of baboons and other animals, therefore new species

As can be noted, a major aspect of Dart's new species was that he felt he had evidence of the earliest use of fire by hominids. This behavioral aspect of the new species cannot be replicated here, but nevertheless, Dart's evidence was never widely accepted, and we may rely on his morphological evidence here (Dart had found a single hominid occipital fragment, and named a new species on it - though again, his belief that fire was used here comprised a major portion of his new species naming).

3.2.5 *Australopithecus (Paranthropus) crassidens* Broom

At the site of Swartkrans, very near Kromdraai (*Paranthropus robustus*) and Sterkfontein (*Plesianthropus transvaalensis*), Broom found another new species, but this time maintained congeneric status with *Paranthropus robustus*. These are the features he felt separated it specifically:

- Broom bases the new species on a single mandible (even states may be new genus)
- teeth are larger than *Paranthropus*, but still similar
- teeth are similar to human but larger
- canine has no deep infolding of the enamel on the lingual side as do those of *Plesianthropus*

Broom extended this diagnosis in 1952 with these traits:

- mandible very massive
- teeth are relatively huge
- originally named *crassidens* on teeth alone, but feels that further evidence from Swartkrans upholds his claim (the evidence was not made clear, however)
- virtually nothing else said to substantiate the different species designation of *Paranthropus crassidens*

In 1954 Robinson reanalyzed the species of the australopithecines. Regarding *Paranthropus crassidens*, he noted:

- the crown and root pattern of the P^3 and the crown pattern of P_3 identical to *P. robustus*
- demarcation of the lower border of the pyriform aperture the same for both *P. crassidens* and *P. robustus*

Robinson felt that there were "no features which contra-indicate referring [*P. crassidens*] to [*P. robustus*]" (Robinson, 1954: 190).

3.2.6 *Telanthropus capensis* Broom and Robinson

Telanthropus capensis was named in 1949 by Broom and Robinson based on a single mandible found at Swartkrans. Although the material of *Telanthropus capensis* was subsequently placed within the genus *Homo*, I will give a brief discussion of it in this study, to highlight the amount of overclassification that went on based on such little material. These are the diagnostic features:

- jaw smaller than human jaws, though 3rd molar larger than any human
- mandibular symphysis runs downwards and slightly backwards, making an angle with the base of the ramus of about 75 degrees
- depth of symphysis about 33mm
- remarkably shallow horizontal ramus
- ascending ramus fairly broad but shallow
- no simian shelf
- mylohyoid groove runs up to the foramen as in human skulls, and is lower down
- teeth appear to be quite human in size
- molars have five cusps and a small sixth is present in all
- 3rd molar is the most different, being the largest
- molars smaller than *Paranthropus* or *Plesianthropus*
- molars of a different pattern than *Paranthropus* or *Plesianthropus* (pattern unidentified)

3.2.7 *Australopithecus (Zinjanthropus) boisei* Leakey

'Zinj' was the first taxonomic entry into the field of paleoanthropology from East Africa. It was named by Louis Leakey in 1959, and though the generic name never really took, the specific distinction did. In the original article Leakey was more concerned about establishing the generic distinction of his new taxon, and therefore listed out only a handful of traits distinguishing it at the specific level (due mainly to the fact that *Zinjanthropus* was a monospecific genus - there were no species to compare it to; nonetheless, he did make some species level comparisons with *Paranthropus robustus*). It was initially based on these observations (made entirely from the only known specimen, OH 5):

- males far more massive than the most massive male *Paranthropus*
- face exceedingly long
- males have sagittal crest, at least posteriorly
- upper third molars smaller than the second

In 1967, Tobias published a landmark monograph on the OH5 skull, listing out every morphological feature he felt was significant. He diagnosed the species, and set out formal criteria defining it. The following are Tobias' important criteria:

- most robust, heaviest construction of the cranium
- calvaria hafted to facial skeleton at low level, giving virtually absent forehead and low supra-orbital height index
- very pronounced ectocranial superstructures and degree of pneumatisation (greater than *robustus*)
- extremely well developed supraorbital torus with twist between medial and lateral components
- well developed sagittal crest
- moderate nuchal crest
- plane of foramen magnum nearly horizontal
- structure of dorsum sellae and sella turcica typically hominine
- cerebellum apparently relatively large
- anterior nasal spine high
- bony face very high and very flat or orthognathous
- nose set in central facial hollow
- ramus of mandible by inference tall and vertical

- jaws very large and extremely robust with powerful development of zygomatic arch, lateral pterygoid plate, temporal crest and temporal fossa
- palate very deep but shelving steeply only in front of the incisive foramen
- premolars and molars extremely large, especially buccolingual dimension
- M3 smaller than M2 in mesiodistal diameter and equal in buccolingual diameter
- maxillary canine absolutely and relatively small and not in harmony with the postcanine teeth
- cingulum remnants or derivatives present on all maxillary molars, weakly developed on buccal surfaces, pronounced on lingual
- sockets of anterior teeth arranged in moderate curve

Tobias felt that *Australopithecus boisei* was distinct enough from *Australopithecus robustus* to warrant fully the generic distinction. He based this on the following morphological criteria:

- the size and especially buccolingual diameters of the cheek teeth, which significantly exceed those of *A. robustus*
- greater disparity between canine and premolar size than in *A. robustus*
- marked reduction of the MD diameter of M^3 as compared with that of M^2 and equality of BL diameters of M^3 and M^2, in both of which respects the Olduvai specimen *A. africanus* and not *A. robustus* (in which both diameters usually increase from M^2 to M^3)
- the morphology of the labial faces of I^1 and I^2, of the lingual face of the canines, and of the crowns of M^1 and M^2 , in all of which the Olduvai specimen approximates to those of *A. africanus*
- the shape, cusp pattern, Carabelli formation, and buccal cingular vestige of M3, all of which are nearer to those of *A. africanus*
- the earlier or more primitive stage in the trend towards reduction of the cingulum, a stage which the Olduvai cranium shares with *A. africanus*, whereas *A. robustus* represents a more advanced stage of reduction, having only weak vestiges of a lingual cingulum and no trace of the buccal cingulum
- curiously foreshortened foramen magnum (which may only be an individual variation)

- more powerful supra-orbital torus
- elongation of the face as a whole and, especially of the nose and the maxilla
- the flexion of the naso-alveolar clivus
- morphology of the zygomatic buttress and the malar notch, and the absence of even the slightest trace of a canine fossa
- nature and extent of the masseteric impressions
- anterior shelving of the palate

Subsequent to this, Rak again redefined *Australopithecus boisei*, once more based on the facial morphology:

- much of the complex topography of *Australopithecus robustus* is completely absent in *Australopithecus boisei*
- no trace of maxillary trigon, zygomaticomaxillary step, or blunt pronounced anterior pillars
- no trace of maxillary fossula, or zygomaticomaxillary fossa
- gentle sweeping transition of zygomatic process, not a sharp corner like *Australopithecus robustus*
- infraorbital region of *boisei* swings around smoothly in a visorlike structure of the face; in *robustus* there is a defined transition between the front aspect of the face and the lateral
- nasomaxillary basin - region on both sides of the upper part of the pyriform aperture forms a concave depression surrounded by a more elevated topography
- inferior orbital margin consists of a relatively sharp rim, unlike the *robustus* sharp/blunt transition
- infraorbital foramen situated rather low in *boisei*, similar to *robustus*
- supraglabellar surface flat and shallow and thus not really a fossa
- most medial part of the supraorbital torus is the highest structure of the facial mask
- upper orbital margins are more or less continuous with the external outline of the frontal process of the zygomatic bone
- orbital shape: steeped parallelogram with highest point at the superomedial corner of orbit (contra *robustus*, *africanus*, apes)
- interorbital area of boisei appears massive and rectangular
- glabella is low compared to superior margins of orbits for "robust" australopithecines
- nasals are very long and narrow

- only the upper margin of the pyriform aperture in *boisei*, that consisting of the nasal bones, and a small segment of the frontal process of the maxilla lateral to them is sharp; farther down, the lateral margin is very blunt
- front surface of the maxilla swings posteriorly toward the nasal cavity and leads to the formation of a vertical wall, forming a corridor (with the other side) leading into the nasal opening
- it is the anterior pillars in *africanus* and *robustus* that leads into the nasal opening, but the walled corridor in *boisei* (which has no anterior pillars)
- also, these walls, and not the pillars that join with the clivus to form the nasoalveolar gutter in *boisei*
- strong upward tapering of the facial mask, more dramatic than *Australopithecus africanus* and *Australopithecus boisei*
- facial height index I (Rak) - measure from supraglabellar region to alveolar plane divided by bi-orbital breadth
- facial height index II (Rak) - measure from supraglabellar region to alveolar plane divided by maximum bizygomatic breadth
- bizygomatic breadth index at plane of orbits
- bizygomatic breadth index - maximum: (ZY-ZY)
- postorbital constriction index - breadth
- temporal foramen index
- zygomaticoalveolar crests appear elongated in *boisei*; added to this is the continuous transition of zygomatic arch
- no zygomatic prominence
- facial height measure: distance between orbitale and occlusal plane
- greater postorbital constriction than either africanus or robustus
- extreme lateral flaring of the zygomatic arches
- lateral flaring and postorbital constriction produce a large temporal foramen (these are all done with the same measures as outlined in *africanus* and *robustus*)
- zygomatic arches show a continuous rounded loop in shape, whereas the *robustus* and *africanus* are more angular (owing to the zygomatic prominence absent in *boisei*)
- sagittal crest formed by the meeting of temporal lines, though not all *boisei* specimens exhibit sagittal cresting
- very small frontal trigon in *boisei*
- palate very deep in anterior as well as posterior part unlike *robustus* in some but not all *boisei*

3.2.8 *Paraustralopithecus aethiopicus* Arambourg and Coppens

This new genus and species was named in 1967 based on one single edentulous mandible found in the Omo Valley in Ethiopia. It was described based on these features:

- general massiveness of the mandible
- considerable thickness of the horizontal ramus
- short length
- parabolic arrangement of the mandible
- shallow mandibular symphysis
- angle of the mandibular symphysis
- considerable reduction of the anterior dentition based on the roots

3.2.9 *Australopithecus afarensis* Johanson, White and Coppens

Named in 1978 by Johanson et al., this was the first new species to be widely accepted since 1959. It marked the beginning of a new splitting trend that continues today. This was also the first species to be named with a strong phylogenetic analysis accompanying it. With its arrival came a newly proposed phylogenetic scheme, also authored by its creators. It was named based on this diagnosis:

- upper central incisors relatively and absolutely large
- upper central and diminutive lateral incisors with strong lingual tuburcles with flexed roots
- strong variation in canine size
- canines asymmetric, lowers with strong lingual ridge, uppers usually with exposed dentine strip along distal edge when worn
- P_3 occlusal outline elongate oval in shape with main axis mesiobuccal to distolingual at 45°-60° to tooth row
- dominant mesiodistally elongate buccal cusp, small lingual cusp often expressed only as inflated lingual ridge

- diastema often present between I2/C and C/P3
- C/P3 complex not functionally analogous to pongid condition
- ascending ramus broad, not high
- corpus of larger specimens relatively deep anteriorly and hollowed in region of low mental foramen which usually opens anterosuperiorly
- moderate superior transverse torus
- low rounded inferior transverse torus
- anterior corpus rounded and bulbous
- strong posterior angulation of symphyseal axis
- postcanine teeth aligned in straight rows
- arcade tends to be subrectangular, smaller mandibles with relatively narrow incisor region
- strong alveolar prognathism with convex clivus
- palate shallow, especially anteriorly
- dental arcade long, narrow, straight sided
- facial skeleton exhibiting large, pillar-like canine juga separated from zygomatic processes by deep hollows
- large zygomatic processes located above P^4/M^1 and oriented at right angles to tooth row with inferior margins flared anteriorly and laterally
- occipital region characterized by compound temporal/nuchal crest (in larger specimens), concave nuchal plane short anteroposteriorly
- large flattened mastoids
- shallow mandibular fossae with weak articular eminences placed only partly under braincase
- occipital condyles with strong ventral angulation

For this species, a number of post-cranial bones were described as well, but since the erect bipedal form of locomotion that typifies modern humans appears to have been in existence for at least 4 million years, and since there is no possible outgroup comparison that can be made, these traits will be left out of this study.

Again, Rak's major work dealt with *Australopithecus afarensis*. Unfortunately at the time, no complete cranium was known, so his diagnosis was based on the fragmentary cranial material known at the time. These were his important morphological features:

- anterior pillars absent, only the canine eminence is present
- very sharp margins clearly demarcate the pyriform aperture; there are no anterior pillars to delimit the edge of the aperture like in *africanus*
- nasal cavity appears as a hollow chamber behind flat maxillary plates
- transverse buttress exists in the infraorbital region, lateral to the pyriform aperture
- canine fossa in the location of the maxillary furrow in africanus
- inframalar notch - notch in the bottom of the zygomaticoalveolar crest not seen in *africanus*
- apparently no zygomatic prominence
- no supratoral sulcus
- distinct sill separates the nasoalveolar clivus from the inferior margin of the pyriform aperture
- nasoalveolar clivus juts forward, and its surface is convex
- impossible to quantify the masticatory system as in the other three species of *Australopithecus* outlined by Rak
- palate is flat and shallow, different from all other hominids and most primates
- the quantification of the masticatory system performed for the other species was not possible for *Australopithecus afarensis* as the remains known a the time were too fragmentary and incomplete

In 1984, Kimbel et al. undertook to reconstruct an *Australopithecus afarensis* skull from the many fragments of skulls that they had collected in Hadar over the years (Kimbel, et al. 1984). Based on this composite reconstruction, they were able to note the following traits possessed by *Australopithecus afarensis*:

- transverse buttress in zygomaticomaxillary region of face
- basinlike canine fossa on lateral face of maxillae

- high frequency of inferosuperiorly and mediolaterally convex premaxillae
- maxillary lateral incisors set partly or entirely lateral to nasal aperture
- relatively large canine (compared to postcanine teeth)
- high frequency of asymmetric unicuspid P_3's
- high frequency of C/P_3 diastemata (mandibular)
- apelike maxillary and mandibular canine wear
- receding anterior mandibular corpus profile
- high frequency of basally set inferior transverse tori
- high frequency of straight or slightly laterally concave mandibular tooth rows
- mental foramen placed low on corpus, usually opening anterosuperiorly
- differential development of posterior temporalis fibers (inferred posterior sagittal crests; compound temporal/nuchal crests in males and some females)
- high occipital scale ratio in males and some females
- development of asterionic notch (strong lateral flare of parietal mastoid angle)
- extensive pneumatization of temporal squama
- strong inferomedial inflection of mastoid process
- very weak articular eminence of mandibular fossa
- flat, very shallow palate

In 1994 a fossil skull was found that belonged to this species, and it gave a clearer idea of the cranial anatomy of the species. These features were found to be diagnostic on the new specimen:

- maxillary postcanine teeth larger than for previous teeth of Hadar/Laetoli, but not unusual
- supraorbital torus vertically thick laterally
- very low squama has neither chimp-like supratoral sulcus, nor a frontal trigone like 'robust' australopithecines
- distance across post-orbital constriction large compared to other australopithecines, both absolutely and relative to facial breadth

3.2.10 *Australopithecus aethiopicus* Kimbel, White and Johanson

In 1986 Richard Leakey discovered a fossil skull that he felt belonged to the species *Australopithecus boisei* (Walker et al., 1986). The date ascribed to the new specimen was 2.5 my, much older than any other known 'robust' specimen. They considered it to be 'robust' because of numerous features it had in common with the other known 'robust' species. In 1988, Kimbel et al. definitely referred the skull, known as KNM-WT17000, to *Australopithecus aethiopicus* (Kimbel et al., 1988). Their reference was based entirely on a cladistic analysis. Of the 32 separate traits that Walker et al. described for the skull, Kimbel et al. found only 2 derived features that were shared exclusively with *Australopithecus boisei*. It also showed 12 derived traits shared with *Australopithecus boisei* and with *Australopithecus robustus*, 2 derived traits shared with both 'robusts' and with *Australopithecus africanus*, and 4 derived traits shared with all post *Australopithecus afarensis* species.

This skull showed not one single autapomorphy, or, traits shared with no other species. Not one single trait defined this species and this one only. In spite of this, and in spite of the numerous traits it held in common with the other 'robust' species, a new species was named. The difficulties of this species were compounded with the actual name, *aethiopicus*. In 1967 a new genus and species were named based on one single edentulous mandible found in Ethiopia, *Paraustralopithecus aethiopicus* (Arambourg and Coppens, 1967). This species never gained acceptance. However, Kimbel et al. associated KNM-WT 17000 with this mandibular fragment, and named their new species (this in spite of the fact they had no mandible for KNM-WT 17000, therefore no comparison). This is a species named for one single skull, and thus seems to preclude the use of any biological concept. This species is not comprised of once living, breeding populations of similar animals. Rather, it is based on a cladistic analysis of a handful of selected traits, owing nothing to any biological reality. Kimbel et al. felt that this new species was required, otherwise "it would, on the same morphological basis, be justifiable to synonimize this species in favor of a broadly defined *Australopithecus robustus*" (Kimbel et al., 1986: 261)."

In any event, the traits that were used to define the new skull, and hence the new species were:

primitive features shared with *Australopithecus afarensis*:
- strong upper facial prognathism
- flat cranial base
- posterior: anterior temporalis large
- temperomandibular joint flat, open anteriorly
- postglenoid process anterior to tympanic plate
- extensive temporal squama pneumatization
- strongly flared parietal mastoid angle (?asterionic notch)
- large horizontal distance between molars and TMJ
- absolutely large anterior tooth row
- maxillary dental arch convergent posteriorly
- flat, shallow palate
- nasion coincident with high glabella

derived features shared with all post- *A. afarensis* species:
- short cranial base
- vertically inclined tympanic plate inferosuperiorly concave
- reduced medial inflection of mastoid process
- nasoalveolar contour projects weakly anterior to bicanine line

derived features shared with *A. africanus*, *A. robustus*, and *A. boisei*:
- maxillary lateral incisor roots medial to nasal aperture margins
- zygomaticoalveolar crest weakly arched in facial view

derived features shared with *A. robustus* and *A. boisei*:

- "dished" midface
- zygomatic process forward relative to palate length
- guttered nasoalveolar clivus grades into nasal cavity floor
- anterior vomer insertion coincident with anterior nasal spine
- nasals widest superiorly
- supraorbitals in form of "costa supraorbitalis"
- receding frontal squama with "trigonum frontale"
- relatively enlarged postcanine tooth row
- incisors in bicanine line
- petrous inclined coronally
- tympanic vertically deep, with strong vaginal process
- mastoid bulbous, inflated beyond supramastoid crest

derived feature shared exclusively with *A. boisei*:

- heart shaped foramen magnum
- temporoparietal overlap at asterion

3.2.11 *Australopithecus ramidus* White, Suwa and Asfaw

The newest fossil hominid species to be named was announced in September of 1994 by Dr. Tim White. He felt it to be the earliest australopithecine species that will ever be discovered, hence the name *ramidus*, which is Afar for "root". A good portion of the diagnosis of the species was devoted to separating it from the apes, the implication being that it is so primitive that some might call it an ape. Once again, traits that separate the australopithecines from the apes will not be analyzed in this study. The species was considered distinct from the other australopithecine species (namely *Australopithecus afarensis*) based on the following:

- upper and lower canines larger relative to the postcanine teeth

- lower first deciduous molar narrow and obliquely elongate, with large protoconid, small and distally placed metaconid, no anterior fovea, and small, low talonid minimal cuspule development
- temperomandibular joint without definable articular eminence
- absolutely and relatively thinner canine and molar enamel
- lower third premolar more strongly asymmetrical, with dominant, tall buccal cusp and steep, posterolingually directed transverse crest
- upper third premolar more strongly asymmetric, with relatively larger, taller, more dominant buccal cusp

3.2.12 *Australopithecus africanus* versus *Australopithecus afarensis*

In 1980, Don Johanson, the discoverer of 'Lucy' and co-namer of *Australopithecus afarensis* listed out a suite of morphological features which he felt separated out the two taxa:

- naso-alveolar clivus (convex vs. flat or concave)
- palate depth
- dental arcade length
- dental arcade straight sided/parabolic
- canine jugae size (anterior buttressing)
- compound temporal/nuchal crest
- mandibular fossa depth
- articular eminence (weak/strong)
- mastoid process size
- mastoid process shape (rounded/bulbous)
- mandibular ramus breadth
- mandibular ramus height
- mandibular corpus depth (especially anteriorly)
- symphyseal axis angulation
- mandibular arcade sub-rectangular vs. sub-parabolic
- mandibular incisor region length
- I^1 size
- mandibular canine lingual ridge development
- P^3 larger than P^4
- diastema at I^2/C
- diastema at C/P_3

Tobias (1980) rebutted Johanson et al (1978) and Johanson (1980). He felt that none of the traits used to diagnose the new taxon were capable of separating *Australopithecus africanus* from *Australopithecus afarensis*, and went trait for trait on 8 cranial, 5 mandibular and 8 dental features:

- "strong alveolar prognathism" - same for many *A. africanus* specimens
- "convex clivus" - same for many *A. africanus* specimens
- "dental arcade long, narrow, straight sided" - same for many *A. africanus* specimens
- "compound temporal/nuchal crest (in larger specimens)" - seen in *A. boisei* as well as possibly in Makapansgat MLD1, plus not in all Hadar specimens - variable development and therefore cannot be used
- "shallow mandibular fossae with weak articular eminences placed only partly under braincase" - these three traits are diagnostic of all australopithecines, and cannot distinguish any from each other
- "occipital condyles with strong ventral angulation" - seen in *A. boisei* and other australopithecines
- "ascending ramus of mandible broad, not high" - seen in *A. africanus* specimens
- "moderate superior mandibular transverse torus" - highly variable character found in many *A. africanus* jaws
- "low rounded inferior mandibular transverse torus" - fits most *A. africanus* mandibles
- "anterior corpus rounded and bulbous" - highly variable trait seen in many *A. africanus* specimens
- "strong posterior angulation of symphyseal axis" - highly variable trait which characterizes most *A. africanus* and *A. robustus* jaws
- "upper central incisors relatively and absolutely large" - measures do not distinguish *A. africanus* and *A. afarensis*
- "diminutive lateral incisors" - *A. africanus* teeth are quite close in size, but in fact are slightly smaller than *A. afarensis*
- "strong variation in canine size" - highly variable trait showing no separation between *A. afarensis* and *A. africanus*

- "canines asymmetric, lowers with strong lingual ridge" - diagnostic feature of *A. africanus*
- "P3 occlusal outline elongate oval in shape w/main axis mesiobuccal to distolingual at 45°-60° to tooth row, dominant buccal cusp, small lingual cusp often expressed only as inflated lingual ridge" - shape described is exactly as seen in Sterkfontein and Makapansgat, therefore no distinction between *A. afarensis* and *A. africanus*
- "postcanine (mandibular) teeth aligned in straight rows" - also found in *A. africanus* therefore not diagnostic

In 1985, Johanson again produced a list of features that he felt were best able to consistently distinguish between *Australopithecus afarensis* and *Australopithecus africanus*:

- *A. afarensis* exhibits a high frequency of mandibular C/P_3 diastemata; rare for *A. africanus*
- upper and lower canines often exhibit pongid-like wear in *A. afarensis*, whereas canine wear is strictly apical in *A. africanus*
- upper and lower anterior teeth in *A. afarensis*, compared with those of *A. africanus*, are relatively larger when compared with to the posterior dental battery
- the P_3 in *A. afarensis* is usually an asymmetrical oval and is unicuspid in males and females; in *A. africanus* P_3 is rounder in shape and bicuspid
- in more advanced stages of cheek tooth wear the lower canines and third premolars of *A. afarensis* project above the tooth row, while in *A. africanus* all teeth are worn flat
- the anterior mandibular corpus is receding and bulbous in *A. afarensis*; in *A. africanus* it is usually straighter and more vertical
- in *A. afarensis* the mental foramen is placed low and opens anterosuperiorly; in *A. africanus* it is at mid-corpus height and opens laterally or slightly anteriorly
- in *A. afarensis* the lateral mandibular surface always bears a shallow depression, posterosuperior to the mental foramen; in *A. africanus* this region is usually swollen. There is some minor overlap, but no *A. afarensis* specimen exhibits the degree of mandibular swelling seen in *A. africanus* and no specimen of *A. africanus* shows the degree of hollowing seen in *A. afarensis*

- in *A. afarensis* there is a high frequency of straight or slightly laterally concave mandibular tooth rows; in *A. africanus* they are laterally convex
- in *A. afarensis* the superior transverse torus is weak to moderate; it is stronger in *A. africanus*
- the transverse buttress on the face of *A. afarensis* is absent in *A. africanus*
- the asterionic notch of *A. afarensis*, previously known only in apes, is absent in *A. africanus*
- in *A. afarensis* the extensive pneumatization of the temporal squama is similar to the ape condition; in *A. africanus* temporal pneumatization is more limited to the mastoid region
- in *A. afarensis* males the canine fossa is so deep it gives a pinched appearance to the face; in *A. africanus* males it is usually reduced to a narrow groove or is absent
- in *A. afarensis* the snout is characterized by a semi-oval outline due in large part to the convex naso-alveolar clivus; in *A. africanus* the clivus is flatter and straighter
- male and females of *A. afarensis* possess compound temporal/nuchal crests similar to those seen in chimpanzees (with or without sagittal crests); this crest is absent in *A. africanus*
- *A. afarensis* has a flat, very shallow palate, while in *A. africanus* it is deeper with premaxillary shelving
- the mastoid process is strongly inflected inferomedially in *A. afarensis* compared with *A. africanus*
- in *A. afarensis* the mandibular fossa is shallow owing to a weak articular eminence; in *A. africanus* the eminence is moderate or strong and hence the fossa is deep
- in basal view the tympanic in *A. afarensis* is tubular and horizontal; in *A. africanus* it is vertical with a strongly curved anterior face
- *A. afarensis* has a high occipital scale ratio (nuchal plane dominance) in males and some females, a condition similar to apes; it is lower in *A. africanus* and only in males is it high
- *A. afarensis* has the steepest nuchal plane of any hominid, whereas in *A. africanus* it is more horizontal

3.2.13 *Australopithecus robustus* vs. *Australopithecus boisei*

In his 1967 volume on *Zinjanthropus*, Tobias listed out a number of morphological features of the OH5 cranium (*Australopithecus boisei*) which he felt set it apart from the South African *Australopithecus robustus*, which essentially separated out the two taxa:

- the size and especially buccolingual diameters of the cheek teeth, which significantly exceed those of *A. robustus*
- greater disparity between canine and premolar size than in *A. robustus*
- marked reduction of the MD diameter of M^3 as compared with that of M^2 and equality of BL diameters of M^3 and M^2, in both of which respects the Olduvai specimen *A. africanus* and not *A. robustus* (in which both diameters usually increase from M^2 to M^3)
- the morphology of the labial faces of I^1 and I^2, of the lingual face of the canines, and of the crowns of M^1 and M^2, in all of which the Olduvai specimen approximates to those of *A. africanus*
- the shape, cusp pattern, Carabelli formation, and buccal cingular vestige of M3, all of which are nearer to those of *A. africanus*
- the earlier or more primitive stage in the trend towards reduction of the cingulum, a stage which the Olduvai cranium shares with *A. africanus*, whereas *A. robustus* represents a more advanced stage of reduction, having only weak vestiges of a lingual cingulum and no trace of the buccal cingulum
- curiously foreshortened foramen magnum (which may only be an individual variation)
- more powerful supra-orbital torus
- elongation of the face as a whole and, especially of the nose and the maxilla
- the flexion of the naso-alveolar clivus
- morphology of the zygomatic buttress and the malar notch, and the absence of even the slightest trace of a canine fossa
- nature and extent of the masseteric impressions
- anterior shelving of the palate

A word must now be given about one of the most prominent of the works cited above. In 1983 Rak published a book detailing the results he had achieved in his doctoral dissertation entitled *The Australopithecine Face*. In this book Rak analyzed the facial structure of the various australopithecine fossils in excruciating detail. Based on this work Rak determined that there were four principle species, *Australopithecus afarensis*, *A. africanus*, *A. robustus*, and *A. boisei*. This work has served as a cornerstone of australopithecine taxonomy ever since. Unfortunately, there are a number of difficulties associated with this work. The primary problem is that it deals almost exclusively with facial anatomical minutiae. The tiniest of differences are selected and treated as if they held great taxonomic significance. While it is granted that the purpose of this current study is to determine whether or not these traits are valid, it is unfortunate that few of the minutiae listed out by Rak are at all reproducible. Most of the differences noted are either not existent at all on primate faces, or are extremely difficult to correlate.

An attempt was made to analyze Rak's various facial morphological features, but it become quite clear early on that there was no way to measure or otherwise duplicate many of Rak's traits. These non-replicable traits were by necessity dubbed autapomorphies, and all autapomorphies were scored as being capable of separating out species. It is apparent that further research is certainly required to determine whether or not such facial minutiae are in fact valid for, and capable of, separating out species of apes. However, such a study is beyond the scope of this work.

3.3 The Genera of the Australopithecines

The different genera of the australopithecines have at various times been subjected to analysis, and have periodically been redefined or even sunk in favor of other genera. Some studies have dealt in depth with the morphological features inherent to the australopithecine genera, and it is these morphological descriptions that will be used in this analysis. It is understood at the outset that the concept of genus is an abstraction, and that different interpretations of the term exist. A genus can be variably (and loosely) defined as either a large enough morphological distinction between groups, or a large enough difference in ecological adaptation. Mayr defines a genus as "consist[ing] of one species, or a group of species of common ancestry, which differ in a pronounced manner from other groups of species and are separated from them by a decided morphological gap" (Mayr, 1950:110). He then goes on to further qualify this definition by stating that "species that are united in a given genus occupy an ecological situation which is different from that occupied by the species of another genus (Mayr, 1950:110)."

The two main points of this definition may be logically interlocked by stating that different adaptive plateaus are likely to produce groups of organisms that are quite different in morphology. This is obviously not always the case as exceptions always apply, but in general this can be thought to hold true. The problem then arises that an insistence on one aspect over the other can nullify any results based on the lesser. If I define a genus as being a large enough morphological gap, my entire thesis can be refuted by stating that in opposition, it is held that genus is merely a different adaptive plateau, and therefore morphology is of dubious value. This logical absurdity cannot be avoided unless a much more precise definition of genus can be attained. From a brief reading of zoological literature, it is apparent that such a definition will not be soon in coming, and in fact will likely never be achieved, again owing to the difference in the two basic points mentioned above.

Since the bulk of all information that paleoanthropologists have to work with is morphological, and since the differentiation of species in this study is based on morphology, I will accept morphological criteria as being capable of separating out genera. That is to say, I define a genus as does Mayr above, that an ecological difference will produce a significant morphological gap, and that such a decided morphological gap can indicate different genera. This is the most logical approach that we can achieve as we have little information regarding the actual ecological adaptations of the australopithecines. Therefore, those traits that were in the past held to be indicative of a generic distinction will be applied to different extant ape genera to determine their actual validity. I will be testing between *Gorilla gorilla* and *Pan troglodytes*, whose close genetical and morphological association has been noted in chapter 1.

Often, new hominid genera were erected for each new species, and therefore the definition of the species and the genus were the same. It becomes very difficult in this situation to define a genus morphologically. For this section of the study, I will alter the strategy somewhat from the section on species. Rather than analyzing every genus erected, I will concentrate on only four genera. First will be *Australopithecus*, the first australopithecine genus named, and to some, the only valid genus. Next will be *Plesianthropus*, the second new genus named in paleoanthropology. *Plesianthropus* is now considered invalid, so a discussion of the exact reasoning for its invalidity will be helpful in our analysis of genera. Next *Paranthropus* will be looked at, and finally *Zinjanthropus*. *Paranthropus* is currently undergoing a resurgence of popularity, with many researchers claiming its taxonomic valence. A thorough discussion of the past as well as some of the current controversy surrounding this genus will help us arrive at a firm decision on its appropriateness as a hominid taxon.

For the genera *Paranthropus* and *Plesianthropus*, diagnoses were rarely performed. Rather, the genera were contrasted against each other, and various traits were discussed as being either present/absent for a genus, or differentially developed. Only *Australopithecus* and *Zinjanthropus* received formal diagnoses. Therefore, only *Australopithecus* and *Zinjanthropus* can be fully analyzed with respect to their formal diagnoses. *Paranthropus* was also briefly described and it too can be analyzed, but its contrasting with *Plesianthropus* represents a different avenue for research. These two genera essentially represent the distinction between the 'robust' and the 'gracile' hominid species. As this is the current point of contention, these two will be contrasted in just this fashion, as 'robust' versus 'gracile'. The features used to distinguish between the two will be analyzed at that level, whether these traits are actually capable of separating out genera. Beyond the discussions of these genera only, Robinson published a great deal of work dealing with his distinction between the 'robusts' and the 'graciles'. These arguments will be incorporated to deal directly with the current issue of whether or not the 'gracile' species should be generically distinct from the 'robust' species, whether both *Australopithecus* and *Paranthropus* are valid taxa.

3.3.1 *Australopithecus* Dart

The genus *Australopithecus* was first named in 1925, and with it began the field of paleoanthropology. Most of the features first described in 1925 applied more to the species than to the genus, and have been treated as such. *Australopithecus* has occasionally come under scrutiny, and its features have been defined on a number of occasions. It is from these descriptions of the genus that its features will be derived. The first discussion of the genus came in 1941 when Broom was discussing the characteristics of a new *Paranthropus* mandible that had been found (Broom, 1941a: 607). Since this mandible was that of a juvenile, direct comparisons could be made between it and the Taungs baby. It was this then that allowed for the first contrasting of *Australopithecus* and *Paranthropus*.

- *Australopithecus* second deciduous incisor larger than *Paranthropus*
- *Australopithecus* deciduous canine smaller than *Paranthropus*
- 1st deciduous molar differs markedly in the shape of the cusps
- 1st deciduous molar differs markedly in the arrangement of the cusps
- 2nd deciduous molar longer and narrower
- 2nd deciduous molar differs in arrangement of cusps

The first complete delineation of *Australopithecus* came in 1946 when Broom published the first Transvaal Museum monograph on the Australopithecinae. He made the following statements about the generic distinction between *Australopithecus* and *Paranthropus* (it must be remembered that only one specimen of *Australopithecus* was known at the time, and it was a juvenile, so all comparisons had to be made with juvenile forms):

- milk teeth of Kromdraai so different from Taung, they must belong to different genus (that is all the justification given)
- the imperfect lower first milk molar of Sterkfontein so different from the same tooth of *Australopithecus*, they must be generically distinct ('nuff said)

In 1954 Robinson began what would become a serious lumping trend. He formally sunk the genera *Plesianthropus* and *Meganthropus*, and referred the material belonging to *Paranthropus crassidens* to *Paranthropus robustus*, thereby sinking *Paranthropus crassidens* as well. He saw the following as representing the genus *Australopithecus* (it must be remembered that Robinson pioneered the movement to distinguish the two genera as representing two very different types of animals, both morphologically and ecologically):

- lower deciduous 1st molar incompletely molarized, protoconid most strongly developed cusp (incl. anterior accessory cusplet) with large sloping buccal surface
- vomer does not insert directly against back of anterior nasal spine
- P3 usually having a single buccal root
- canines large with mandibular canine strongly asymmetrical and lingual ridge present, normally strongly developed

- skull narrow, forehead present, supraorbital torus not strongly developed

In 1955 Le Gros Clark published a landmark volume in which he outlined the traits that he felt defined the genus *Australopithecus* (revised in 1964):

- cranial capacity ranging from 450cc to well over 600cc
- strongly built supra-orbital ridges
- supra-orbital height index of about 60
- tendency in larger individuals to form low sagittal crest in frontoparietal region of the vertex of the skull (but not associated with the nuchal crest)
- occipital condyles well behind the midpoint of the cranial length but on a transverse level with the auditory apertures
- nuchal area of occiput restricted, as in *Homo*
- consistent development of a pyramidal mastoid process typical of hominid form and relationships
- mandibular fossa constructed on the hominid pattern but in some individuals showing a pronounced development of the postglenoid process
- massive jaws showing considerable individual variation in respect of absolute size
- mental eminence absent or slightly indicated
- symphyseal surface relatively straight and approaching the vertical
- dental arcade parabolic in form with no diastema
- spatulate canines wearing down flat from the tip only
- relatively large premolars and molars
- anterior lower premolar bicuspid with subequal cusps
- pronounced molarization of the first deciduous molar
- progressive increase in size of permanent lower molars from first to third

In 1967 Tobias published his landmark volume on the OH 5 skull, *Zinjanthropus*. The first conclusion that he came to when discussing the taxonomy of the australopithecines was that

Zinjanthropus did not represent a valid taxon separate from *Australopithecus* (Tobias, 1967: 219), echoing the previous statement made by Leakey et al. (1964) that the name *Zinjanthropus* be formally sunk in favor of *Australopithecus*. He then proceeded to define the genus *Australopithecus* as follows:

- relatively small cranial capacity, with an average about 500 c.c. and an estimated population range of 360 to about 640 c.c.
- a relatively thin walled cranium rendered robust in parts by strong ectocranial superstructures and by marked pneumatization
- strongly built supra-orbital ridges
- moderate to fairly high orbits, with a lower mean height than in pongids
- a tendency in individuals with larger cheek teeth for the formation of a low sagittal crest in the frontoparietal region of the calvaria (but the sagittal crest is not continuous with either the nuchal crest or the occipital torus, whichever is present)
- occipital condyles well behind the anteroposterior midpoint of the cranial length, but in the same coronal plane as the external acoustic apertures
- foramen magnum well forward on the base of the cranium
- planum nuchale of occipital bone rising only a short distance above the Frankfurt Horizontal and generally facing downwards much more than backwards
- inion low and generally close to the Frankfurt Horizontal plane
- a low nuchal crest not continuous with the sagittal crest in heavier toothed forms, and a slight occipital torus in moderate toothed forms
- consistent development (in immature as well as mature crania) of a pyramidal mastoid process of typical hominine form and relationships
- a mandibular fossa which is shallow and mediolaterally broad, but is otherwise constructed on the hominid pattern, especially in the slopes and curvature of the anterior wall and the upward slope of the preglenoid plane, but with a pronounced entoglenoid process and, in some individuals, a moderate development of the postglenoid process
- porion elevated in position above the nasion-opisthion line

- massive and robust jaws, showing marked individual variation in respect of absolute size
- mental eminence absent or slightly indicated
- symphyseal surface relatively straight and retreating
- contour of internal mandibular arch V-shaped or blunt U-shaped
- dental arcade parabolic in form with no diastema
- moderate sized, spatulate canines wearing down flat from the tip only
- relatively large premolars and molars, the enlargement being more marked in the buccolingual diameter of the crown
- lower anterior premolar bicuspid with subequal cusps
- pronounced molarization of the lower 1st deciduous molar
- progressive increase in size of permanent lower molars from the 1st to the 3rd, but M^3 is commonly smaller than M^2

Robinson expanded this list in 1968, using the following traits:

- endocranial volume of the order of 450-550cc
- distinct forehead, but never markedly developed
- bony face moderately - not completely - flat
- distinction between floor of nasal cavity and subnasal maxillary surface present but poor
- zygomatic arch moderately developed
- temporal fossa of medium size
- palate of more or less even depth
- sagittal crest normally absent - may occur in extreme cases
- internal mandibular arch contour V-shaped
- ascending ramus usually sloping backward and of moderate height
- tooth row compact, no diastema
- anterior and postcanine teeth harmoniously proportioned
- canines wear down from the tip, moderately large in all known cases
- incompletely molarized dm_1, anterior fovea displaced lingualward and open to that side
- maxillary incisor and canine sockets in parabolic curve

The most recent rediagnosis of *Australopithecus* was performed by Wolpoff and Lovejoy in 1975. They found these features to be diagnostic:

- very large cranial capacity, with range from under 400cm^3 to over 900cm^3, average of 500cm^3
- heavily pneumatized cranial base
- weakly to moderately developed supraorbital torus
- extremely well developed muscles of mastication frequently leading to the development of a low sagittal crest generally beginning anterior to or at bregma in males or more robust individuals
- widely flared zygomatics
- large temporal fossae
- an anterior position of the zygomatic process of the maxilla with the anterior root of the zygoma arising between C and M1 (and the consequent appearance of facial flattening)
- tendency for the appearance of a frontal trigone
- massive jaws, especially in the robustness of the corpus, but varying considerably in absolute size
- vertical ascending ramus and symphyseal region
- superior and inferior transverse tori present with a horizontally elongated post-incisive plane
- massive post-canine dentition relative to body size with a tendency towards multiple or accessory cuspation in both deciduous and permanent posterior teeth (dm1 consistently molarized)
- moderately large anterior dentition with distinct sexual dimorphism in canine size
- progressive molar size increase from M1 to M3
- large and prognathic face

3.3.2 _Plesianthropus_ Broom

Plesianthropus was initially named in 1938 by Broom to illustrate what he considered to be a generic distinction between the Sterkfontein materials and the Taung skull. He had originally called the Sterkfontein fossils *Australopithecus transvaalensis*, but two years later decided that they belonged in different genera, so *Plesianthropus* was created. It was named based on these features:

- the shape of the [mandibular] symphysis is so different from that of the Taungs ape that it seems advisable to place *A. transvaalensis* in a distinct genus, for which the name *Plesianthropus* is proposed

It can clearly be seen that this new genus was named on the flimsiest of evidence. This is where the difficulty in diagnosing *Plesianthropus* arises. It cannot be performed on one single morphological trait. Not by any stretch of the imagination could this be considered diagnostic of an entire new genus. The only other arguments that were put forward in favor of the status of *Plesianthropus* were those that contrasted it directly with *Paranthropus*, and it is for this reason that the two must be analyzed together (see below).

3.3.3 *Paranthropus* Broom

The first *Paranthropus* remains found were those of *Paranthropus robustus*, discovered by Robert Broom in 1938 at the site of Kromdraai. The original discovery had been made by a young schoolboy, but it was Broom's recognition of the importance of the teeth that lead to the creation of the new genus and species. A further skull was uncovered, and briefly described in 1938. Broom made only two comparisons to his other genus, *Plesianthropus*:

- extremely small canine tooth, clearly very unlike the canine of *Plesianthropus transvaalensis*; this statement was made despite the fact the crown of the tooth was missing

- 2nd premolar differs very markedly from that of *Plesianthropus transvaalensis*, and we may thus confidently place the new skull in a new genus and species

The genus *Paranthropus* was sunk in 1964 in favor of *Australopithecus* (Leakey et al., 1964). However, not all accepted this sinking as being valid. John Robinson held the opinion that there was a sufficient difference between the 'gracile' and 'robust' australopithecines, both morphologically and ecologically, that a generic distinction was warranted. In a groundbreaking paper in 1954, Robinson revised the taxonomy of the australopithecines, and helped to deliver it from some of the confusion it suffered from due the over-classification that had occurred in the early period of activity. In this work, Robinson expounded his ideas about the separation of the australopithecines into euhominids (which were later to be attributed to *Homo*) and prehominids (the australopithecines). Robinson formally sank *Plesianthropus* into *Australopithecus*, and *Meganthropus* into *Paranthropus*. He further sank the Makapan material (*Australopithecus prometheus*) and the Sterkfontein material (*Plesianthropus transvaalensis*) into *Australopithecus africanus*, retaining the species names of the former as subspecies thereof; and the Swartkrans material (*Paranthropus crassidens*) was sunk into the Kromdraai taxon *Paranthropus robustus*, again with a subspecific distinction. Robinson defined *Paranthropus* as such:

- dm_1 strongly molarized, metaconid and hypoconid largest cusps, protoconid without large, sloping face
- vomer does insert against back of anterior nasal spine

- P3 usually with double buccal roots (i.e. three roots all together)
- canines small, mandibular one not strongly asymmetrical, lingual ridge never strongly developed
- skull broad across ear region, no forehead, supraorbital torus well developed near midline

In 1968, Robinson expanded this diagnosis, as many further fossil finds had become known. He added:

- endocranial volume of 450-550cc
- forehead completely absent
- supra-orbital height index of about 50 (average for pongids)
- bony face either quite flat or actually dished
- distinction between floor of nasal cavity and subnasal maxillary surface totally absent
- zygomatic arch strongly developed
- temporal fossa large
- palate appreciably deeper posteriorly than anteriorly
- sagittal crest normally present in both sexes
- internal mandibular arch contour V-shaped
- ascending ramus vertical and high
- tooth row compact without diastema
- anterior teeth very small compared to postcanine teeth
- canine small and wears down from the tip
- virtually completely moralized dm$_1$ with anterior fovea centrally situated and with complete margin
- maxillary canine and incisor sockets in almost straight line across front of palate

In 1985, Clarke was spearheading an effort to have the genus *Paranthropus* reinstated as a valid genus of early hominid. He listed out the following features as separating *Paranthropus* from *Australopithecus* (which he felt was easier to separate than was *Homo* from *Australopithecus*):

- a brain that is on average larger than that of *Australopithecus*, yet not as large as that of *Homo*
- formation of a slightly concave, low forehead with a frontal trigone delimited laterally by posteriorly-converging temporal crests
- presence of a flattened 'rib' of bone across each supra-orbital margin
- a glabella that is situated at a lower level than the supra-orbital margin
- formation of a central facial hollow associated with a completely flat nasal skeleton, and a cheek region that is situated anterior to the plane of the pyriform aperture
- naso-alveolar clivus sloping smoothly into the floor of the nasal cavity
- small incisive canals that open into the horizontal surface of the nasal floor
- great enlargement of premolars relative to molars and canines
- great enlargement of molars and massiveness of tooth-bearing bone
- anterior teeth small when compared to premolars and molars
- a tendency for the maxillary canine and incisor sockets to be situated in an almost straight line across the front of the palate
- formation on the naso-alveolar clivus of prominent ridges marking the central incisor sockets, but concavities marking the lateral incisor sockets
- cusps of cheek teeth low and bulbous and situated closer to the center of the crown than in other hominid genera
- formation of flat occlusal wear surfaces to the cheek teeth, accompanied by smoothly rounded borders between the occlusal surfaces and sides of the crowns of the cheek teeth
- virtually completely molarized dm_1 with anterior fovea centrally situated and with complete margin
- great increase in the size of the masticatory musculature and attachments relative to the size of the skull
- temporal fossa capacious and mediolaterally expanded
- formation of a broad gutter on the superior surface of the posterior root of the zygoma
- a tendency for the palate to be shallow anteriorly and deep posteriorly
- formation of either a marked pit or a groove across the zygomaticomaxillary suture of the cheek region - at least in South African *Paranthropus*

3.3.4 *Zinjanthropus* Leakey

Leakey named his new 1959 find *Zinjanthropus boisei*, and spent a great deal of time discussing those traits he felt warranted a generic distinction from *Australopithecus* and *Paranthropus*. He felt the following were taxonomically and anatomically important:

- in males the nuchal crest is developed as a continual ridge across the occipital bone
- inion set lower than in *Australopithecus* and *Paranthropus* (despite great muscularity) in Frankfurt horizontal
- posterior wall of the occipital bone rises more steeply to form, within the parietals, a very high vaulted posterior region of the skull
- foramen magnum less elongate and has more horizontal position than in *Australopithecus* (no equivalent structure preserved in any *Paranthropus* samples)
- presence of a very massive horizontal ridge or torus above the mastoids (much more marked than normal type of supra-mastoid crest)
- mastoids are more similar to those seen in present day man, both in size and shape
- presence of a strong wide shelf above the external auditory meatus, posterior to the jugal element of the temporal bone
- the shape and from of the tympanic plate, whether seen in norma lateralis or in norma basilis
- very great pneumatosis of the whole of the mastoid region of the temporal bones, which even invades the squamosal elements
- the massiveness of the jugal element of the temporal bone relative to the total size of the temporal bone
- the way in which the parietals rise almost vertically behind the squamous elements of the temporal before bending over to become a dome
- relative thinness of the parietals in comparison with the occipitals and temporals
- very prominent and keeled anterior margin of the crest on the frontal bone for the anterior segment of the temporal muscles in the region of the post-orbital constriction (even most muscular male *Paranthropus* shows nothing comparable)

- very unusual position of the nasion, which on the most anterior part of the skull, instead of being behind and below glabella
- very great absolute and also relative width of the inter-orbital area, with which may be associated the shape of the nasal bones, which are much wider at the top than at their inferior margin
- the whole shape and position of the external orbital angle elements of the frontal bone
- very deep palate more like *Homo* than is *Australopithecus*, and quite unlike the form seen in *Paranthropus*
- the conformation of the malar-maxillary area of the cheek; in *Australopithecus* and *Paranthropus* there is a buttress of bone from malar to alveolar region near 4th premolar - this buttress absent in Zinj
- very great area of muscle attachment on the inferior margin of the malars
- relatively greater reduction of canines in comparison with the molar premolar series than is seen in *Paranthropus*

Almost immediately Robinson took issue with the new genus, and argued trait for trait against 'Zinj'. These are the traits he highlighted:

- inion lower relative to Frankfurt horizontal: it is in fact similar to both *Australopithecus* and *Paranthropus* , almost exactly in the Frankfurt plane
- posterior of occipital forms high vault: similar to *Paranthropus* , less so in *Australopithecus*
- *Paranthropus* has an almost spheroidal brain case which is relatively low and narrow anteriorly, but steep-sided and higher posteriorly - Zinj is similar to this
- *Australopithecus* has a brain-case more similar to dolichocephalic modern hominine
- nasion almost coinciding with glabella: this is true in *Paranthropus* and in some cases of *Australopithecus* ; in *Paranthropus* and Zinj, nasals are relatively very wide near the nasion
- very great absolute and relative width of inter-orbital area: cannot be separated from *Australopithecus* , *Paranthropus* , or *Homo*, therefore not taxonomic valence

- very deep palate: in *Paranthropus* and Zinj the palate slopes (different between anterior and posterior depths) with more depth posterior; different from *Australopithecus* & *Homo*
- zygomatic process of maxilla: Zinj has poorly developed zygomatic, similar to that seen in South African specimens
- greater reduction of canines compared to pre/ and molars: falls within *Paranthropus* range for a ratio of modules of pre-molars and molars
- sagittal crest occupies exact same position as *Paranthropus* in Zinj - roughly the middle third of the distance between inion and glabella
- anterior teeth set along straight line across the front of the palate very reduced, while post-canines appreciably larger
- Zinj clearly fits well within *Paranthropus* range, as a slightly more robust type of animal; though not out of the range of other primates
- proposes that Zinj be called *Paranthropus boisei*

As can be seen by the last point, Robinson felt there might be a specific distinction between the two, but not a generic one. This was the attitude of most researchers, and the species came quickly to be known as either *Australopithecus* or *Paranthropus boisei*, until 1967, when Tobias rediagnosed it, and definitely referred it to *Australopithecus*.

3.3.5 *Ardipithecus* White, Suwa and Asfaw

The most recent genus to be named in the field of paleoanthropology is *Ardipithecus* of White et al., named in 1995. The diagnosis of the new genus is based on the new *Australopithecus ramidus* materials from Ethiopia. It is identical to the species diagnosis, with no new traits or information given. Essentially the species *ramidus* was transferred to a new genus. No reasons were given for the move, but will presumably be forthcoming. It is apparent that White et al. (1995) believe their finds to be different at the generic level, rather than belonging in the genus *Australopithecus*. Therefore, the diagnosis of the genus is identical to that of the species (which is automatic for any monospecific genus):

- upper and lower canines larger relative to the postcanine teeth
- lower first deciduous molar narrow and obliquely elongate, with large protoconid, small and distally placed metaconid, no anterior fovea, and small, low talonid minimal cuspule development
- temperomandibular joint without definable articular eminence
- absolutely and relatively thinner canine and molar enamel
- lower third premolar more strongly asymmetrical, with dominant, tall buccal cusp and steep, posterolingually directed transverse crest
- upper third premolar more strongly asymmetric, with relatively larger, taller, more dominant buccal cusp

3.3.6 *Australopithecus/Plesianthropus* vs. *Paranthropus*; or 'Robust vs. 'Gracile'

The second hominid genus to be named was *Plesianthropus*, erected to accommodate the Sterkfontein fossil material. *Plesianthropus* is now considered invalid, so it is of extreme interest in this study, particularly as a comparative model for the current controversy over the recent move to reinstate *Paranthropus* as a valid genus. As we have seen, Broom named the new genus on some rather flimsy evidence. Subsequent comparisons were performed, mainly with *Paranthropus* (as again, *Australopithecus* at the time consisted of only one specimen, the Taungs skull). In Broom's 1946

Transvaal Museum monograph, he indicated the following as being traits that distinguished between the genera *Paranthropus* and *Plesianthropus*:

- *Plesianthropus*: face not flattened, no anterior pillars
- *Plesianthropus*: the large outer cusp of the 2nd lower premolar is completely united with the small posterior
- first upper molars in *Plesianthropus*, the crown is almost square with rounded corners
- *Plesianthropus*: main inner cusp is deeply cut into behind by the continuation forwards of the posterior foveal groove; this does not occur in *Paranthropus*
- in *Plesianthropus* the foramen magnum is farther back than in *Paranthropus* (measure distance from foramen magnum to foramen ovale)
- lower canine of *Plesianthropus* larger than *Paranthropus*, measured both at the base and at the crown, as well as for height
- in *Plesianthropus*, large sphenoidal sinus at base of pterygoid; there seems to be no sinus here in *Paranthropus*
- brain of *Paranthropus* is very appreciably larger than *Plesianthropus*
- incisors appear to be much smaller in *Paranthropus* than in *Plesianthropus*, both upper and lower
- premolars of *Paranthropus* are much larger than *Plesianthropus*; opposite as seen for incisors and canines
- 2nd lower premolar: *Paranthropus* larger than *Plesianthropus*
- *Paranthropus*: the antero-external cusp of 2nd lower premolar is cut off from the small postero-external by a furrow which , on the outer side of the tooth, forms a marked groove
- second upper molars are similar, but *Paranthropus* are more rhomboidal
- third upper molars: the postero-internal cusp (hypocone) in *Plesianthropus* is large (forming a third of the crown), while in *Paranthropus* it is small (less than a quarter of the crown)
- third lower molars between the two there is considerable agreement, though in *Plesianthropus* the indications of the inner cingulum are more marked than in *Paranthropus* (though only one *Paranthropus* tooth to compare existed at the time)
- first upper molars in *Paranthropus*, the crown is rhomboidal

- *Paranthropus*: infraorbital portion of the face is nearly flat (cheeks are as far forward as the nose)
- *Paranthropus*: bony ridge from infra-orbital foramen to front socket of the canine (sounds closest to anterior pillar)

In 1954, as earlier mentioned, Robinson iterated his reasons for calling *Australopithecus* and *Paranthropus* separate genera. Since only one hominid fossil has ever been found at Taungs, *Australopithecus* was made up mostly of *Plesianthropus* fossils at the time, which Robinson had just sunk into *Australopithecus*. Therefore, for the purpose of this section we can treat *Australopithecus* and *Plesianthropus* as synonymous, and we can validly compare the two genera as *Plesianthropus* versus *Paranthropus*. Robinson listed the following as reasons for the separation of the two genera:

- lower deciduous molar in *Australopithecus* smaller than *Paranthropus*, with 5 cusps, though hypoconulid is small; in *Paranthropus* the tooth is fully molariform with 5 well developed cusps of equal size
- in *Australopithecus* the entoconid of lower deciduous molar is a small cusp well separated from the protoconid
- in *Australopithecus* the anterior fovea of the lower deciduous molar is a large depressed area lingual to the metaconid
- in *Paranthropus* the vomer inserts into the back of the anterior nasal spine, in *Australopithecus* it does not
- sharp demarcation between maxilla and pyriform aperture in *Australopithecus*; demarcation in *Paranthropus*, but not as marked (divide, but not a sill)
- roots of P^3 double in *Paranthropus*, but single in *Australopithecus*
- *Paranthropus* has small canines (upper and lower), very similar to modern human canines, with asymmetrical crown; in *Australopithecus* the canines are larger and more symmetrical
- in *Australopithecus* a very strong lingual ridge present in mandibular canine
- in *Australopithecus* the skull is narrow with an unmistakable forehead and a weakly developed supra-orbital torus

- in *Paranthropus* the skull is slightly larger, broad across the ear region, has no real forehead, and a well developed supra-orbital torus
- facial prognathism usually more marked in *Australopithecus* than in *Paranthropus*
- sexual dimorphism appears more marked in *Australopithecus* than in *Paranthropus*

In 1956 Robinson produced another of the landmark Transvaal Museum series of volumes, this time on the dentition of the australopithecines. In it he analyzed and compared all the known hominid fossils of *Australopithecus*, *Paranthropus*, *Pithecanthropus* and *Sinanthropus*, as well as modern humans. Based on his very detailed study of the australopithecine teeth, he came up with the following traits which he felt distinguished *Australopithecus* from *Paranthropus*:

- maxillary bicanine line in *Australopithecus* curved, while in *Paranthropus* straight
- maxillary incisors very similar in all euhominids as well as prehominids
- mandibular incisors - prehominids all fall well within the range found in modern man as in maxillary incisors
- canines of *Australopithecus* symmetrical, with a well defined apex; not so in *Paranthropus*
- *Paranthropus* has smaller canines than *Australopithecus*
- *Paranthropus* has upper premolars (P^3 and P^4) which are appreciably larger than *Australopithecus*
- *Australopithecus* is more closely related to euhominids than *Paranthropus* based on premolar size
- P^3 buccal grooves lightly developed in *Paranthropus* , but well defined in *Australopithecus*
- *Paranthropus* premolars show 3 roots, while *Australopithecus* shows 2 roots
- in *Australopithecus* the talonid of P^4 is never well developed, while in *Paranthropus* a distinct distal buccal cusp (=talonid) is present

- *Paranthropus* P_3 more rounded, less asymmetrical, and has a less well defined lingual cusp; *Australopithecus* P_3 asymmetrical and well developed lingual cusp
- *Paranthropus* P_4 larger in P than in *Australopithecus*
- *Australopithecus* maxillary molars smaller than *Paranthropus*
- M^3 usually larger than M^2 in *Paranthropus* , but M^3 smaller than M^2 in *Australopithecus*
- *Australopithecus* mandibular molars smaller than *Paranthropus*
- in *Paranthropus* mandible, molar size increases $M1<M2<M3$, while in *Australopithecus* $M1<M2>M3$
- *Paranthropus* molars nearly oval in shape, while *Australopithecus* more rectangular
- only one deciduous specimen with incisors and canines known for *Paranthropus*, therefore no definitive comparisons can be made
- deciduous lower 1st molar talonid small in *Australopithecus*, talonid cusps poorly developed; *Paranthropus* with large talonid with well developed cusps
- deciduous lower 1st molar has well developed anterior fovea in *Australopithecus*, displaced lingualward; smaller anterior fovea in *Paranthropus*, centrally placed
- deciduous lower 1st molar mesial cuspule present in *Australopithecus*, not in *Paranthropus*

All of the preceding traits will be analyzed in the next two chapters to determine their actual ability to separate out extant primate species. The different diagnoses provided for each taxon will be lumped together into single encompassing lists for the different species and genera.

Chapter 4 - Trait Separation for *Pan troglodytes* and *Pan paniscus*

4.1 Introduction

In this section the actual analysis of the primate material will be performed on the lists of traits outlined in chapter 3. Each hominid species will be looked at individually to determine the taxonomic validity of each of the traits used to define that species. Once again, every trait regarded as being capable of separating out hominid species will be applied to extant primate species, in this case *Pan troglodytes* and *Pan paniscus*, to ascertain if those traits are able to statistically separate the modern chimpanzees.

Data on the chimpanzees were collected during the months of October and November of 1994 at a number of museums in the U.S.A. The following specimens were studied from the indicated museums:

Table 2. Specimens Utilized in Study

Cleveland Museum of Natural History

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	12	14	1	10
Pan paniscus	2	2	3	0

American Museum of Natural History

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	9	7	0	12
Pan paniscus	0	1	0	2

National Museum of Natural History

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	4	4	0	9
Pan paniscus	0	0	0	1

Harvard Museum of Comparative Zoology

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	0	0	0	0
Pan paniscus	2	1	0	0

Total Chimpanzee Specimens Collected

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	25	25	1	31
Pan paniscus	4	4	3	3

Unfortunately, mandibles were available for only 6 of the *Pan paniscus* specimens. This caused some difficulty in analysis which will be covered below.

Juvenile and adult skulls will be analyzed together. The ages of the ape specimens in this study were determined by a combination of the information recorded on the animals when collected, as well as a dental age assessment. In the case of a disagreement, the dental age was accepted as valid to keep more in line with the age assessments of fossil hominids. The juvenile skulls were those that showed the M3's almost coming into occlusion. Adults were those which showed M3's in occlusion, and with some wear of the teeth. These specimens will be scored together because in virtually every diagnosis presented on any hominid species, the only age separation presented was between adult and infant, specifically between deciduous and permanent dentition. No age separation was indicated as being taxonomically important between adult and juvenile. The sex of the infant skulls was in some cases not made available, and since no determination of the sex of these specimens could be reliably made, it was ignored for all specimens. Again, dental ages were attached to the animals, and infants were those which still maintained their deciduous dentition. Those specimens which were transitional between infant and juvenile dental ages were excluded from this study for greater clarity of age dependent analysis.

In total, 51 *Pan troglodytes* specimens were studied, and 11 *Pan paniscus*. Of the 11 *Pan paniscus* skulls, 7 were casts made at the Cleveland Museum of Natural History. The extreme paucity of *Pan paniscus* material in North America necessitated a high reliance on casts, as well as some rather small sample sizes as compared to the *Pan troglodytes* numbers. However, since the Cleveland Museum of Natural History is world renowned for its excellence in the casting of primate specimens, it was assumed that these casts were of top quality and were exact replicas of the originals. Care was also taken to ensure that the casts had not been made from any of the original *Pan paniscus* skeletal materials studied by this author. The small number of *Pan paniscus* skulls could not be overcome, as every specimen that could be found in the eastern U.S. was measured.

All measurements were performed with standard skeletal measuring devices, including a digital Vernier caliper, spreading calipers, coordinate calipers, a depth gauge, and a mandibulometer board. Specimen selection was carried out as thoroughly as possible. In the case of the American Museum of Natural History every chimpanzee in the collection in the Mammalogy department was measured, unless it was clearly pathological. A number of gorilla specimens were also randomly selected. In the National Museum of Natural History, every gorilla was measured unless it was too damaged to provide any results. As many of the chimpanzee skeletons were measured as time allowed, again in as random a fashion as possible. The Harvard Museum of Comparative Zoology possesses three *Pan paniscus* skeletons which were all measured. The Hamann-Todd collection at the Cleveland Museum of Natural History provided the largest collection. As the individual specimens there were independently collected, randomness was assured. The only directed selection was an attempt to achieve parity with regards to sex.

4.2 Metric Versus Discrete Traits

There are essentially two types of data which may be collected from skeletal specimens. The first are the metric traits, those which are readily quantifiable. These include anything which can be measured such as cranial length, aperture width, tooth size, etc. The second type are non-metric and involve making judgments on the relative development of certain discrete structures, such as anterior buttress or supra-orbital torus development. These are not so readily quantifiable, and require comparative assessments to be made. Although there have been criticisms made of the use of such minor morphological variations (Carpenter, 1976; Corruccini, 1974), many accept them as being valid and quite useful in the analysis of differing populations (Berry, 1976; Berry and Berry, 1967; Green et al., 1979; Ossenberg, 1977; Molto, 1979, 1983). The use of such non-measurable traits will be accepted as valid in this study; that is to say, this author accepts that discrete or discontinuous traits are potentially capable of separating out species. What this study purports to look at is whether or not the particular traits selected by past researchers are capable of doing so.

The two forms of data also require two different forms of statistical manipulation. Since continuous metric traits are numerical, they are quite amenable to simple parametric statistical analyses. In the case of this study, the Student's t-test will be employed for the metric traits. The discontinuous, non-metric traits will require a non-parametric test. The simplest and most elegant of the non-parametrics is the chi-square test, and it is this test that will be used for the non-metric traits. The use of each, and their justification will be discussed below.

For the purpose of this thesis, the program StatView 4.0® has been utilized for most statistical manipulations, while a select few manipulations required particular setup and analysis in Microsoft Excel 4.0®.

4.2.1 Metric Data - The Student's T-Test

The Student's t-distribution was initially discovered by William S. Gossett in 1908 but, being an employee of the Guinness brewery in Dublin, he was not allowed to publish his work under his own name. He chose the pseudonym Student for his landmark publication, and it has stuck ever since. The Student's t-test allows for a comparison of the means of two samples, even though the variance of the population is not known. This is important in that the variance of a biological population can realistically never be known for certain. Variance is the average dispersion of variates about the mean of the population. Variates are individual measures of each variable. We can never really know just how the distribution of the variates around a mean will look, so a test which does not require such information is very important.

The t-test tests whether a noted difference is due to a real difference between the populations or whether the disparity between the samples should be attributed to chance alone (Thomas, 1986:235). Differences in size are especially agreeable to testing by this method. If two samples come from significantly different populations, the t-test will uncover this fact. The t-test is a very robust test when applied to non-normally distributed populations, a fact which has been borne out by numerous experiments (Thomas, 1986:256).

The t-distribution itself is very similar to the normal distribution, though with a somewhat different shape depending on the number of degrees of freedom. Above 30 degrees of freedom the t-distribution is essentially the same as the normal distribution (Sokal and Rohlf, 1969:144). As an approximation of the normal distribution, the t-test is of great value in biometry. In fact, some believe the t-test to be the best approximation for testing the differences between two samples (Simpson, et al. 1960:183). This is the reasoning behind the selection of this particular test for this study. It is a robust test when it comes to unknown variances or non-normal distributions, which are very likely in the samples of primates drawn for this thesis. It is easy to perform and, just as importantly, it is easy for the reader to understand. The t-test essentially tests whether or not the means of two samples are drawn from the same or different populations.

For the majority of the testing, a two-tailed test was sufficient to determine the statistical difference. The two-tailed t-test is useful for separating non-directional hypotheses, i.e. those which do not imply a particular increase or decrease in size. One-tailed testing may be applied when a directional change is implied. For example, the statement "increase in size from M^1 to M^3" indicates that the teeth become larger as we move posteriorly. This implies more than just a difference in size. The teeth becoming larger requires a slight modification for testing. Only one tail of the t-distribution need be looked at, since we are concerned only with an increase in size. This has the effect of doubling the level of the critical region for statistical acceptance, making it more difficult to reach. Essentially, this method tests whether the probablity value exceeds a certain threshold (the critical region) on one side only of the probability distribution.

4.2.2 Non-Metric Data - The Chi-Square Test

One of the most commonly used tests in anthropology is the chi-square test. The chi-square statistic is very simple to use and understand. It is a non-parametric test, and non-parametrics differ from parametrics in two critical assumptions. Non-parametrics do not assume interval or better measurement, and they do not assume a normal distribution, both of which must be met in parametrics. The main value of the chi-square for this study is that it is capable of testing the non-metric data that was collected. The chi-square tests whether there is a statistically significant association between two samples; essentially whether the development of a trait in one sample is the same as or different from that of another sample. In this case I will test whether the traits selected are able to separate the two species of chimpanzee, or whether there is such a statistical association between them that they cannot be distinguished from each other.

The chi-square is similar to the t-test in that it tests whether two populations can be statistically separated from each other. The chi-square is also a good test to use when sample sizes are small. However, the situation can arise where the sample size is too small to provide reliable results. In such a case a modification of the chi-square, the Fisher's exact test, can be applied. The chi-square distribution is estimated by a continuous curve, and the values obtained for this test are compared to this curve at discrete intervals to approximate the expected value. This approximated value falls between two intervals on a statistical table, and it is from this that the probability statements are made. The Fisher's exact test on the other hand derives the exact probability of contingency tables by adding all the potential probabilities (Thomas, 1986:291). The advent of fast and easy to use computers and programs has facilitated much greater ease in statistical workings. Whereas the computations previously required to determine the Fisher's exact test made it quite difficult to use, the use of the computer makes it much more feasible. Owing to the fact that the sample size of *Pan paniscus* material was so small in this study, the Fisher's Exact value was calculated for every trait used to distinguish between *Pan paniscus* and *Pan troglodytes*.

Some of the chimpanzee data collected for this study were in the form of multiple levels of development. For example, the supra-orbital torus development was scored for weak, moderate and well developed, and this required a larger (e.g. 2x3, 2x4) contingency table be constructed. This situation is difficult to test with the Fisher's exact method which requires a 2x2 contingency table for computation. Where the test was set up in a 2x3 contingency table, the Fisher's exact could not be reliably performed. Therefore, a reduction in cells was required for small sample sizes occasionally encountered with the *Pan paniscus* material. The recommended procedure is to collapse two columns into one (Simpson et al., 1960:323). This was done only for the data collected on the two species of chimpanzee, since some of the sample sizes were necessarily small. These required the Fisher's Exact test for greater certainty. The sample sizes for the *Pan troglodytes* versus *Gorilla gorilla* were sufficiently large to allow for multiple contingency (RxC) tables.

In every case, the collapsing was done so that the minimal expression of a trait was compared to all other levels of development. For example, the supra-orbital torus was compared in its state of weakest development against the moderate and strong development which were collapsed together as a level of development above the minimal expression of the trait. In this manner the Fisher's exact test could be performed with a minimal loss of information. The higher levels of development were merely arbitrary distinctions, while the minimal expression of a trait was the closest to non-arbitrary as possible; collapsing the higher levels was the most logically consistent method.

All statistical manipulations appear in the appendices at the end of this thesis. They are divided into four sections: **Appendix A**) metric data - t-tests performed on all measurements for all species, *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla*; **Appendix B**) non-metric data - chi-square tests performed on all comparisons between *Pan troglodytes* and *Pan paniscus*; **Appendix C**) non-metric data - chi-square tests performed on all comparisons between *Pan troglodytes* and *Gorilla gorilla*; **Appendix D**) tables of all raw data.

4.3 Trait Separation

All of the traits that were noted in chapter 3 have been compiled into lists, each species or genus being defined by one list. The traits have been analyzed using the statistical procedures outlined above to determine their validity. Each species has been divided into four categories: metric traits which separate out, metric traits which do not separate, non-metric traits which separate out, and non-metric traits which do not provide separation. A final category of "autapomorphic or non-replicable traits" will be added to encompass those features which represented a unique morphological trait or those which could not be replicated in a study of ape skeletal morphology.

Many of the points listed in chapter 3 for the various species actually indicated more than one trait. For example, in the definition of the species *Australopithecus afarensis*, the point "arcade tends to be subrectangular, smaller mandibles with relatively narrow incisor region" was noted. This point actually comprises three traits, including subrectangular dental arcade, small mandibular size, and narrow incisor region. Whenever this occurred, the procedure adopted was to split the point into its constituent parts, and analyze each separately. For this reason, some of the lists compiled in this chapter will be different than those seen in chapter 3.

Each species and genus has been studied independently to determine the ability of its ascribed traits to separate out extant apes statistically. They have been analyzed in the exact order in which they appeared in chapter 3. It must be again noted that this chapter will be looking exclusively at the specific status of the australopithecines, with no attention being given to which genus the species belong to. The genera will be dealt with in the next chapter.

4.3.1 *Australopithecus africanus* Dart

Metric Data - Different Populations

- ramus of mandible of moderate height
- slender mandibular ramus
- jaws (maxillae) of moderate size (maxillary jaw index)
- forward situated foramen magnum, gives head-balancing index similar to human (bipedal trait)
- lack massive canines/canines large
- nasal aperture small and just wider than it is high (nasal aperture index)
- glabella-inion length shorter than chimps and gorillas (glabella-opisthocranion length separates out chimp species)
- palate of more or less even depth

- mandibular canine larger than in other species, and more in harmony with the postcanine teeth
- premolars not markedly expanded buccolingually (BL breadth)
- molars not markedly expanded buccolingually (BL breadth)
- premolars of moderate size (dental module)
- molars of moderate size (dental module)
- bony face orthognathous to markedly prognathous
- maxillary M^3 equal to M^2 in buccolingual diameters
- orbits circular, not sub-rectangular
- bi-orbital breadth
- forehead present (supra-orbital height index)

Non-metric Data - Different Populations

- supraorbital torus not strongly developed
- no nasal spine
- vomer does not insert directly against back of anterior nasal spine
- well developed anterior fovea on first lower permanent molar
- zygomatic prominence present (pronounced bulbous corner on the zygomatic arch)
- distinct ridgelike sill separates the nasoalveolar clivus from the nasal cavity, at the inferior margin of the nasal opening
- sockets of anterior teeth arranged in a moderate to marked curve
- no posterior fovea on first lower permanent molar

Metric Data - No Separation

- skull narrow (eu-eu)
- short length of nasal bones
- nasal bones widen inferiorly and are usually flat on the same (coronal) plane (nasals widen inferiorly for both *paniscus* and *troglodytes* - one sided t-test)
- palate relatively deep (measured between P^4 and M^1)
- palate shelving steeply in front of the incisive foramen (the palate shelves steeply for both *paniscus* and *troglodytes* - one sided t-test)
- mandibular M_3 smaller than M_2 in mesiodistal diameters (M_2 larger than M_3 in both species of chimp)
- maxillary M^3 smaller than M^2 in mesiodistal diameters (for both *paniscus* and *troglodytes* the M^3 is significantly smaller than M^2, therefore no separation evident - one tailed t-test)
- mandibular M_3 equal to M_2 in buccolingual diameters
- enhanced relationship of cerebral length to facial length to accommodate larger brain (not bone) - Cerebral/facial Index

- facial height index I (Rak) - measure from supraglabellar region to alveolar plane divided by bi-orbital breadth
- facial height index II (Rak) - measure from supraglabellar region to alveolar plane divided by maximum bizygomatic breadth
- bizygomatic breadth index at plane of orbits (Rak)
- bizygomatic breadth index - maximum: (ZY-ZY) (Rak)
- postorbital constriction index - breadth (Rak)
- temporal foramen index (Rak)
- calvaria hafted to facial skeleton at high level, giving forehead and high supra-orbital index
- ramus of mandible sloping somewhat backward
- cranium markedly dolichocephalic (cranial index separates out species)

Non-metric Data - No Separation

- glabella tolerably pronounced (on Taung skull)
- nasal bones are not prolonged below the level of the lower orbital margins, completely fused in the lower half
- nasal bones sharp superior, blunt inferior
- rounded lateral margins of the pyriform aperture, therefore not distinctly demarcated like *Homo* (buttress rounding into aperture)
- sagittal crest commonly absent though probably present in some individuals (this may be an autapomorphy, though it is entirely physiological - no crests seen in any chimps)
- nuchal crest not present, but slight to moderate occipital torus commonly present
- supraorbital tori do not descend medially, but merge to a prominent glabella
- cingulum remnants or derivatives present on all maxillary molars, weak on buccal, pronounced on lingual (cingulum remnants found on some, but certainly not all, maxillary molars of both species)
- deciduous canine without mesial cusplet/deciduous canine with mesial cusplet
- degree of moralization of lower first deciduous molar less complete
- lower deciduous 1st molar protoconid most strongly developed cusp (incl. anterior accessory cusplet) with large sloping buccal surface
- diastema between canines and lateral incisors of the upper jaw
- no diastema between premolars and canines on lower jaw
- mandibular M_1 posterior fovea absent

- anterior pillars present
- mandibular canine strongly asymmetrical
- mandibular canine lingual ridge present, normally strongly developed
- tuberculum sextum present on maxillary M^1/M^1 without tuberculum sextum

Autapomorphic or Non-Replicable traits

- incisors do not project forward (autapomorphy)
- jaw has parabolic arrangement (autapomorphy)
- no simian shelf (autapomorphy)
- maxillary furrow present (modified form of the canine fossa - autapomorphy)
- anterior pillars and nasoalveolar clivus stretched between them form a nasoalveolar triangular frame elevated from the rest of the face(autapomorphy)
- zygomaticoalveolar crest - inferior margins of the zygomatic process; angles down from top to dental arcade \/ (horizontal in apes and humans - autapomorphy)
- wide flaring of the zygomatic arch; measure max. bi-orbital width, max. width of zygomatics, and divide the two to get an index; much larger in *Australopithecus* (autapomorphic condition)
- nasal region slightly elevated from the facial plane (autapomorphy)
- supra-orbital region not separated from the squama by supratoral sulcus (all chimps possess supratoral sulcus)
- P3 usually having a single buccal root (could not test root development)

The taxon *Australopithecus africanus* was defined by a total of 72 separate traits (see Table 2). Of these 72 traits 26, or 36%, were capable of separating out the two species of chimpanzee, while 36, or 50%, were not able to distinguish between the two species of chimpanzee. Ten, or, 14% of the traits were either autapomorphic or non-replicable. Only one of these traits was non-replicable as a result of the research design of this study (root development could not be tested). Therefore, 9, or, 13% of the traits were autapomorphic, and as such, validly separate the species *Australopithecus africanus* from all others. Adjusting for this, we conclude that 49% of all traits listed for *Australopithecus africanus* were valid traits, while 50% were not.

Table 3. *Australopithecus africanus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	18	25
Non-metric data, separate populations	8	11
Metric data, no separation	18	25
Non-metric data, no separation	18	25
Autapomorphic traits	9	13
Non-replicable traits	1	1
Total	72	100

4.3.2 *Australopithecus (Plesianthropus) transvaalensis* Broom

Metric Data - Different Populations
- canine relatively small
- cranial capacity (of specimen) 600cc.

Non-metric Data - Different Populations
- moderately developed brow ridges

Metric Data - No Separation
- 1st molar moderately large
- 2nd molar exceptionally large

Non-metric Data - No Separation
- 2nd molar with four large cusps
- 2nd molar with well marked posterior fovea (for both max and mand)
- 3rd molar with three well developed cusps and small hypocone due to large fovea - wrinkled crown (hypocone <1/4 size; also max M3 post fovea size)

Autapomorphic or Non-Replicable Traits
- fairly large frontal sinuses (require disarticulated frontal bone)

Australopithecus (Plesianthropus) transvaalensis was described based on a total of 9 traits (see Table 3). Of these, 3, or 33%, were capable of separating out the chimpanzees, while 5, or 55%, were incapable of doing so. There was one non-replicable trait, representing 11% of the total combined traits, which could not be studied, and which therefore is excluded from this tabulation. The extreme paucity of character traits for this taxon makes it of dubious value, and when it is further noted that the majority of traits were invalid for discrimination, it can be safely concluded that this taxon does not represent a valid species, and was rightly sunk in 1954.

Table 4. *Australopithecus (Plesianthropus) transvaalensis* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	2	22
Non-metric data, separate populations	1	11
Metric data, no separation	2	22
Non-metric data, no separation	3	33
Autapomorphic traits	0	0
Non-replicable traits	1	11
Total	9	99

4.3.3 Australopithecus (Paranthropus) robustus Broom

Metric Data - Different Populations

- maxillary M^3 commonly larger than M^2 in buccolingual diameters
- crown of P_4 appreciably larger than that of P_3 (*P.robustus*) - mandibular
- relatively small canines
- incisors relatively small; laterals scarcely larger than centrals
- bony face of low to moderate height
- ramus of mandible very high
- mandible large and robust (mandibular size index, index of robusticity)
- maxillary jaws (palate) large and robust (maxillary jaw size index)

- palate deeper posteriorly than anteriorly
- mandibular canine absolutely and relatively small and not in harmony with postcanine teeth (canine to postcanine indices)
- considerable post-orbital constriction
- glabella and nasion appear to be either overlapping or in great proximity
- bony face flat or orthognathous
- palate relatively short
- premolars and molars of very large size
- post orbital constriction very pronounced
- cranial capacity approx. 600 cc (Kromdraai skull)

Non-metric Data - Different Populations

- moderate or marked supra-orbital torus with no twist between the medial and lateral components
- sockets of anterior teeth arranged in a low to moderate curve
- zygomatic prominence - greater height of zygomatic in *robustus* leads to an elongated zygomatic prominence over *africanus* that extends downwards from the inferior orbital margins
- inferior margins of the pyriform aperture lack the sharp sill that separates the nasoalveolar clivus from the floor of the nasal cavity in *africanus*; the transition thus is rather smooth
- small nuchal crest commonly present
- cingulum remnants only weakly represented on lingual face and absent on buccal face of maxillary molars
- supraglabellar fossa below the level of the torus between the orbits
- deciduous maxillary canine symmetrical (*P.r.robustus*)
- deciduous maxillary canine with very small distal cusplet (*P.r.robustus*)
- sockets of anterior teeth arranged in a low to moderate curve
- sharp inferior edges of the nasals merge inferolaterally into the blunt lateral margins of the pyriform aperture and become obliterated (like in *africanus*)

Metric Data - No Separation

- mandibular M_3 commonly larger than M_2 in buccolingual diameter
- mandibular M_3 commonly larger than M_2 in mesiodistal diameter
- maxillary M^3 commonly larger than M^2 in mesiodistal diameter
- calvaria hafted to the facial skeleton at low level, with absent forehead and low supra-orbital index
- palate shelves gradually from the molar region forwards

- facial height index I (Rak) - measure from supraglabellar region to alveolar plane divided by bi-orbital breadth
- facial height index II (Rak) - measure from supraglabellar region to alveolar plane divided by maximum bizygomatic breadth
- bizygomatic breadth index at plane of orbits
- bizygomatic breadth index - maximum: (ZY-ZY)
- postorbital constriction index - breadth
- temporal foramen index
- ramus of mandible vertical (mandibular angle)

Non-metric Data - No Separation

- sagittal crest formed as result of union of the two inferior temporal lines (sagittal cresting absent in all chimps, present in all male gorillas; also temporal lines converge)
- inferior margins of orbits - medial part extremely sharp, lateral part blunt; the transition between sharp and blunt and the thin sections is abrupt
- supraorbital torus shows arched orbits
- supraorbital torus follows shape of superior margins of orbits, and is continuously uniform
- nasoalveolar clivus mostly flat (curvature of clivus)
- frontal trigon - that part of the frontal bone surface not covered by the temporal muscles; shallow basinlike appearance in *robustus*
- only slight anterior tapering seen in the post canine dentition, almost parallel (postcanine tooth row shape)
- anterior pillars; the width and degree of upward extension of the anterior pillar toward the frontal bone appear larger in *robustus* than *africanus*
- anterior pillar's elevation above the bone surface next to it (the zygomatic process) in *robustus* modest compared to *africanus*
- face appears to have upwardly tapering contour, much like *africanus*; extends from inferior part of root of zygomatic arch up
- dm1 with no mesiobuccal cusplet anterior to anterior fovea (*P.r.robustus*)/dm1 with mesiobuccal cusplet (*P.r.crassidens*)
- deciduous lower canine markedly asymmetrical
- deciduous lower canine with distal cusp well developed (*P.r.crassidens*)
- degree of moralization of lower first deciduous molar more complete

- tympanic bone situated mainly below the posterior glenoid process
- occipital condyle in practically the same plane as the external auditory meatus
- palate anteriorly narrowed
- premolars without marked cusps

Autapomorphic or Non-Replicable traits

- nose set in central facial hollow (autapomorphy)
- zygomaticomaxillary step (sort of a second anterior pillar, just under the orbits) (Rak - autapomorphy)
- zygomaticomaxillary fossa (groove crossing the zygomaticomaxillary step in the lower third in all individuals) (Rak - autapomorphy)
- maxillary trigon - gutterlike triangular shape to infraorbital region betweenanterior pillar and zygomaticomaxiallry step (Rak - autapomorphy)
- infraorbital foramen appears very low on the anterior surface of the maxilla close to the inferomedial corner of the trigon, contrasted to *africanus'* more normal position (autapomorphy)
- maxillary fossula - elongated fovea found near alveolar end of anterior pillar (Rak - autapomorphy)
- subforamen divide - bone table of the maxillary trigon surface completely separates the infraorbital foramen and the maxillary fossula (Rak - autapomorphy)
- zygomaticomaxillary step appears to continue topographically into medial thin segment of orbital margins (Rak - autapomorphy)
- no sign of a supratoral sulcus (same as *africanus*) (autapomorphy - all chimps possess supratoral sulcus)
- zygomatic prominence constitutes lateral profile, instead of anterior pillars in africanus, in the upper face (dished face - autapomorphy)
- the sockets for the canines and the incisors are usually on the same line as the mesial face of P3 for the species (autapomorphy)
- nasoalveolar gutter - lower part of clivus found on same coronal plane as anterior pillars; closer to pyriform, more sunken relative to pillars (autapomorphy)
- root of P4 double (couldn't look at roots) (*P.robustus*)

The species *Australopithecus (Paranthropus) robustus* was defined using 71 separate traits (see Table 4). Of these 71 traits, 28, or 40% were capable of distinguishing between the two species of chimpanzee, while 30, or 42% were incapable. Twelve of the traits, totaling 17%, were autapomorphic, while 1, or, 1% was non-replicable owing to research design (tooth roots were not studied). Pooling these autapomorphic and discriminatory traits then, we see that 40 traits, equal to 57% of the total number of traits, were capable of separating *Australopithecus (Paranthropus) robustus* from all other taxa.

Table 5. *Australopithecus (Paranthropus) robustus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	17	24
Non-metric data, separate populations	11	16
Metric data, no separation	12	17
Non-metric data, no separation	18	25
Autapomorphic traits	12	17
Non-replicable traits	1	1
Total	71	100

4.3.4 *Australopithecus prometheus* Dart

Metric Data - Different Populations
- low lying inion (basion - inion)
- elevated opisthocranion (glabella - opisthocranion)
- occipital bone with its expanded planum occipitale (=nuchal plane index)
- reduced planum nuchale (nuchal crest size, nuchal plane index)

Non-metric Data - Different Populations

Metric Data - No Separation

Non-metric Data - No Separation

Non-Replicable Traits

- thickened bone of skull - based on the occipital bone of one individual (could not test bone thickness)
- paedomorphic torus occipitalis (could not test paedomorphosis)
- retardation of sutural obliteration and the concomitant expansion of the tempero-parieto-occipital association areas of the brain; Dart indicates that it may be an adult *A. africanus*, but says Taungs infant had uncomplicated occipital sutural system; sutura mendosa, and parieto-occipital system of sutural ossifications (could not test sutural patterns)
- also discusses the importance of the "evidence" of fire use and ODK hunting of baboons and other animals, therefore new species

The taxon *Australopithecus prometheus* was named on 7 morphological traits. Four of these were able to separate the two species of chimpanzee (57%), while 3 (43%) were untestable. The last item used to define the new species was the evidence Raymond Dart felt he had of the earliest use of fire. The few traits that do separate the species are not enough evidence by any standard to name a new species, and Dart was quite aware of this. Therefore, he relied most heavily on his presumed cultural evidence. Unfortunately, the evidence he had of fire was proven actually to be manganese staining, and not fire. His other cultural evidence, the osteodontokeratic culture, was also later proven to be incorrect (Brain, 1958). Robinson had sunk *Australopithecus prometheus* in 1954 on morphological grounds, and since the bulk of Dart's evidence lay with the ODK, when it fell, *prometheus* sank with it. The minimal evidence seen here as validating the species is clearly insufficient to name a new biologically valid taxon.

Table 6. *Australopithecus prometheus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	4	57
Non-metric data, separate populations	0	0
Metric data, no separation	0	0
Non-metric data, no separation	0	0
Autapomorphic traits	0	0
Non-replicable traits	3	43
Total	7	100

4.3.5 *Australopithecus (Paranthropus) crassidens* Broom

Metric Data - Different Populations

- molars are much bigger; teeth are larger than *Paranthropus robustus*, but still similar
- mandible very massive

Non-metric Data - Different Populations

Metric Data - No Separation

Non-metric Data - No Separation

- canine has no deep infolding of the enamel on the lingual side as do those of *Plesianthropus*
- *P. crassidens* had the identical deciduous molar tooth pattern as *P. robustus*, namely lower deciduous molar is fully molariform with 5 well developed cusps of equal size
- the crown and root pattern of the P^3 and the crown pattern of P_3 identical to *P. robustus*
- demarcation of the lower border of the pyriform aperture the same for both *P. crassidens* and *P. robustus*

Autapomorphic or Non-Replicable Traits

- Broom originally named *crassidens* on teeth alone, but felt that further evidence from Swartkrans upheld his claim (unspecified, therefore non-replicable)

Australopithecus crassidens was named on extremely flimsy evidence, comprising 6 traits only. Of these 2 or, 33%, were able to distinguish between the species of chimpanzees, while 4 or, 67%, were not. Although there is a suite of traits which may be used to define members of *Australopithecus crassidens*, the majority are traits which are quite similar to *Australopithecus robustus*. This lead Robinson to exclaim that there were "no features which contra-indicate referring [*P. crassidens*] to [*P. robustus*] (Robinson, 1954: 190)." Grine (1981, 1984, 1985) believed he had discovered a list of traits which showed conclusively that *Australopithecus crassidens* was a valid species, separate from *Australopithecus robustus*. However, these traits all deal with the dental microwear patterns of the deciduous dentition of the australopithecines, and as such, do not appear to be sufficient to determine a biologically valid species. Also, dental microwear patterns were beyond the scope of this study.

Table 7. *Australopithecus crassidens* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	2	33
Non-metric data, separate populations	0	0
Metric data, no separation	0	0
Non-metric data, no separation	4	67
Autapomorphic traits	0	0
Non-replicable traits	0	0
Total	6	100

4.3.6 <u>*Telanthropus capensis* Broom and Robinson</u>

<u>Metric Data - Different Populations</u>
- jaw smaller than human jaws (mandible size index)
- depth of symphysis about 33mm
- remarkably shallow horizontal ramus
- ascending ramus fairly broad but shallow

- molars smaller than *Paranthropus* or *Plesianthropus*; teeth appear to be quite human in size (overall tooth size)

Non-metric Data - Different Populations

Metric Data - No Separation
- mandibular symphysis runs downwards and slightly backwards, making an angle with the base of the ramus of about 75 degrees
- 3rd lower molar is the most different, being the largest; 3rd lower molar larger than any human

Non-metric Data - No Separation
- molars have five cusps and a small sixth is present in all

Autapomorphic or Non-Replicable Traits
- no simian shelf (autapomorphy)
- mylohyoid groove runs up to the foramen as in human skulls, and is lower down (autapomorphy)
- *Telanthropus* upper canine roots smaller than *Paranthropus crassidens* (root patterns could not be studied)
- both *Telanthropus* and *Paranthropus crassidens* have three roots, but in *Paranthropus crassidens* the mesiobuccal root may fuse with the lingual (root patterns could not be studied))
- molars of a different pattern than *Paranthropus* or *Plesianthropus* (pattern unidentified - non-replicable)

The taxon *Telanthropus capensis* was again named on extremely little evidence, this time based entirely on a single mandible. Although the majority (5, or 39%) were able to separate out the two species of chimpanzee, the extreme paucity of traits again militates against too great a reliance on their ability to determine the validity of this species. Five traits capable of separating the taxa, plus 2 autapomorphies, are not enough to determine a valid species. It must also be remembered that the original namer of the taxon retracted his nomen, and referred the material to *Homo erectus*.

Table 8. *Telanthropus capensis* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	5	39
Non-metric data, separate populations	0	0
Metric data, no separation	2	15
Non-metric data, no separation	1	8
Autapomorphic traits	2	15
Non-replicable traits	3	23
Total	13	100

4.3.7 *Australopithecus Zinjanthropus boisei* Leakey

Metric Data - Different Populations

- extremely well developed supraorbital torus with twist between medial and lateral components
- plane of foramen magnum nearly horizontal (head balance index)
- bony face very high (supra-orbital index)
- ramus of mandible by inference tall
- mandible extremely robust (index of robusticity)
- mandible very large (mandibular size index)
- maxillary jaws very large (maxillary jaw index)
- premolars of extremely large size, especially buccolingually
- molars of extremely large size, especially buccolingually
- maxillary M^3 equal to M^2 in buccolingual diameters
- maxillary canine absolutely and relatively small and not in harmony with the postcanine teeth
- facial height measure: distance between orbitale and occlusal plane
- greater postorbital constriction than either *africanus* or *robustus*
- bony face very flat or orthognathous
- cerebellum apparently relatively large

Non-metric Data - Different Populations

- anterior nasal spine high (nasal spine size)
- sockets of anterior teeth arranged in moderate curve
- supraglabellar surface flat and shallow and thus not really a fossa
- interorbital area of *boisei* appears massive
- no zygomatic prominence
- moderate nuchal crest

- cingulum remnants or derivatives present on all maxillary molars, weakly developed on buccal surfaces, pronounced on lingual

Metric Data - No Separation

- calvaria hafted to facial skeleton at low level, giving virtually absent forehead and low supra-orbital height index
- palate shelving steeply only in front of the incisive foramen
- palate very deep (palate depth between P^4&M^1 - between M^2&M^3 significant)
- ramus of mandible by inference vertical (mandibular angle)
- mandibular M_3 equal to M_2 in buccolingual diameters
- mandibular M_3 smaller than M_2 in mesiodistal diameters
- maxillary M^3 smaller than M^2 in mesiodistal diameters
- nasals are very long
- nasals are narrow (superior; inferior is significant)
- facial height index I- measure from supraglabellar region to alveolar plane
- facial height index II- measure from supraglabellar region to alveolar plane
- bizygomatic breadth index at plane of orbits
- bizygomatic breadth index - maximum: (ZY-ZY)
- postorbital constriction index - breadth
- lateral flaring and post-orbital constriction produce a large temporal foramen (temporal foramen index)

Non-metric Data - No Separation

- well developed sagittal crest (no chimps have crest; physiological trait, but perhaps autapomorphy)
- sagittal crest formed by the meeting of temporal lines, though not all *boisei* specimens exhibit sagittal cresting (temporal lines converge)
- very small frontal trigon in boisei
- inferior orbital margin consists of a relatively sharp rim, unlike the *robustus* sharp/blunt transition
- most medial part of the supraorbital torus is the highest structure of the facial mask (medial descent of torus - doesn't separate)
- interorbital area of *boisei* appears rectangular (interorbital area shape)
- glabella is low compared to superior margins of orbits for "robust"australopithecines (glabella WRT orbits)
- only the upper margin of the pyriform aperture in *boisei*, that consisting of the nasal bones, and a small segment of the

frontal process of the maxilla lateral to them is sharp; farther down, the lateral margin is very blunt

- gentle sweeping transition of zygomatic process, not a sharp corner like *robustus* (neither sweep nor corner is sig.)
- no blunt pronounced anterior pillars (anterior buttress development)
- it is the anterior pillars in *africanus* and *robustus* that leads into the nasal opening, but the walled corridor in *boisei* (which has no anterior pillars)
- strong upward tapering of the facial mask, more dramatic than *africanus* and *boisei*
- zygomatic arches show a continuous rounded loop in shape, whereas the *robustus* and *africanus* are more angular (owing to the zygomatic prominence absent in *boisei*) (sweeping of Zygomatic; also zygomatic arch corner)
- males have sagittal crest, at least posteriorly

Autapomorphic or Non-Replicable traits

- nose set in central facial hollow (autapomorphy)
- no trace of maxillary trigon, zygomaticomaxillary step (Rak - autapomorphy)
- no trace of maxillary fossula, or zygomaticomaxillary fossa (Rak - autapomorphy)
- zygomaticoalveolar crests appear elongated in boisei; added to this is the continuous transition of zygomatic arch (autapomorphy)
- infraorbital region of *boisei* swings around smoothly in a visorlike structure of the face; in *robustus* there is a defined transition between the front aspect of the face and the lateral (Rak - autapomorphy)
- nasomaxillary basin - region on both sides of the upper part of the pyriform aperture forms a concave depression surrounded by a more elevated topography (Rak - autapomorphy)
- front surface of the maxilla swings posteriorly toward the nasal cavity and leads to the formation of a vertical wall, forming a corridor (with the other side) leading into the nasal opening (Rak - autapomorphy)
- also, these walls, and not the pillars that join with the clivus to form the nasoalveolar gutter in *boisei* (Rak - autapomorphy)
- extreme lateral flaring of the zygomatic arches (Rak - autapomorphy)
- upper orbital margins are more or less continuous with the external outline of the frontal process of the zygomatic bone (Rak - autapomorphy)

- orbital shape: steeped parallelogram with highest point at the superomedial corner of the orbit (Rak - autapomorphy contra *robustus*, *africanus*, apes)
- structure of dorsum sellae and sella turcica typically hominine (couldn't test cranial internal structures)
- very pronounced degree of pneumatization (couldn't test as most *Pan paniscus* were casts)

Australopithecus Zinjanthropus boisei was defined based on 64 different traits, 22 or 34.5% of which were able to differentiate the two species of chimpanzee. Twenty-nine, or 45.5%, of the traits could not separate the two chimpanzees. However, when the numerous autapomorphic conditions noted by Rak are included, the number of separating traits is elevated to 33, or 51.5%. We can therefore see that the numerous facial morphological minutiae illustrated in *The Australopithecine Face* require corroboration. Although many authors have considered the two taxa, *Australopithecus robustus* and *Australopithecus boisei* to be conspecific (Skelton et al., 1986; Johanson et al., 1979) or at least members of a superspecies (Tobias, 1968), the results of this analysis are, as of yet, equivocal. It would still appear that the species *Australopithecus boisei* was validly distinguished from all other australopithecine species.

Table 9. *Australopithecus Zinjanthropus boisei* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	15	23.5
Non-metric data, separate populations	7	11
Metric data, no separation	15	23.5
Non-metric data, no separation	14	22
Autapomorphic traits	11	17
Non-replicable traits	2	3
Total	64	100

4.3.8 *Paraustralopithecus aethiopicus* Arambourg and Coppens

Metric Data - Different Populations

- general massiveness of the mandible (mandible size index)
- short length of mandible
- shallow mandibular symphysis
- angle of the mandibular symphysis

Non-metric Data - Different Populations

Metric Data - No Separation

- considerable thickness of the horizontal ramus (Mandibular index of robusticity)

Non-metric Data - No Separation

Autapomorphic or Non-Replicable Traits

- considerable reduction of the anterior dentition based on the roots (did not look at roots)
- parabolic arrangement of the mandible (autapomorphy)

With *Paraustralopithecus aethiopicus* we again see a species being named for one single mandible, in this case one not even possessing teeth. A few traits of the mandible were capable of separating out the two species of chimpanzee, but again, the diagnostic criteria are so flimsy and inconsequential that the validity of the species cannot be accepted. Of the 7 traits which defined the species, 4, or 57%, were able to separate the chimpanzees, while 1, or 14%, were incapable. One trait, again 14% of the total traits, was autapomorphic, and therefore 5 traits, 71%, separated the species. Again, however, we see only a handful of traits which would be difficult to accept as a valid species. No one accepted this species as being valid until Kimbel et al. (1988) resurrected it to allow for the naming of their species *Australopithecus aethiopicus*. Even the original namers considered it to be a *nomen nudum* (Coppens, 1980).

Table 10. *Paraustralopithecus aethiopicus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	4	57
Non-metric data, separate populations	0	0
Metric data, no separation	1	14
Non-metric data, no separation	0	0
Autapomorphic traits	1	14
Non-replicable traits	1	14
Total	7	99

4.3.9 *Australopithecus afarensis* Johanson, White and Coppens

Metric Data - Different Populations

- upper central incisors relatively and absolutely large
- mandibular corpus of larger specimens relatively deep anteriorly and hollowed in region of low mental foramen which usually opens anterosuperiorly (mandibular corpus height)
- anterior corpus rounded and bulbous (mandibular index of robusticity)
- distance across post-orbital constriction large compared to other *Australopithecus*, both absolutely and relative to facial breadth
- dental arcade long (ol-sta)
- dental arcade narrow (enm-enm)
- palate is flat
- mandible with relatively narrow incisor region
- smaller mandible (Mandibular Index of Robusticity; Mandibular Size Module)
- ascending ramus broad, not high
- relatively large canine (compared to postcanine teeth)

Non-metric Data - Different Populations

- shallow mandibular fossae
- concave nuchal plane short anteroposteriorly (nuchal crest size)
- apparently no zygomatic prominence
- no supratoral sulcus

- distinct sill separates the nasoalveolar clivus from the inferior margin of the pyriform aperture
- occipital region characterized by compound temporal/nuchal crest
- high frequency of unicuspid, asymmetric P_3's

<u>Metric Data - No Separation</u>

- strong variation in canine size (CoV very high for both spp.)
- strong posterior angulation of symphyseal axis (symphyseal angle no sep., but this may be an autapomorphy in that the angulation is posteriorly directed, not anteriorly like apes)
- palate shallow, especially anteriorly

<u>Non-metric Data - No Separation</u>

- maxillary dental arcade straight sided (postcanine tooth row shape)
- mandibular postcanine teeth aligned in straight rows (postcanine tooth row shape)
- facial skeleton exhibiting large, pillar-like canine .juga separated from zygomatic processes by deep hollows (anterior buttresses and canine fossae respectively)
- large mastoids
- flattened mastoids
- mandibular fossae with weak articular eminences
- canines asymmetric (mand and max)
- lower canines with strong lingual ridge
- mandibular P_3 dominant mesiodistally elongate buccal cusp, small lingual cusp often expressed only as inflated lingual ridge
- diastema often present between (maxillary) I^2/C and (mandibular) C/P_3
- mandibular arcade tends to be subrectangular
- supraorbital torus vertically thick laterally
- no frontal trigone like robust *Australopithecus*
- transverse buttress exists in the infraorbital region, lateral to the pyriform aperture
- nasoalveolar clivus surface is convex
- nasoalveolar clivus juts forward (alveolar prognathism)
- large zygomatic processes located above P^4/M^1
- zygomatic processes oriented at right angles to tooth row
- mental foramen placed low on corpus, usually opening anterosuperiorly (all apes show this)
- differential development of posterior temporalis fibers - inferred posterior sagittal crests

- transverse buttress (weak vs. all other expressions because always present)
- maxillary lateral incisors set partly or entirely lateral to nasal aperture (all apes show this)

Autapomorphic or Non-Replicable Traits

- zygomatic processes with inferior margins flared anteriorly and laterally (autapomorphy)
- very sharp margins clearly demarcate the pyriform aperture (one of Rak's traits - autapomorphy)
- nasal cavity appears as a hollow chamber behind flat maxillary plates (dished face - autapomorphy)
- development of asterionic notch (strong lateral flare of parietal mastoid angle) (autapomorphy)
- basinlike canine fossa (autapomorphy)
- receding anterior mandibular corpus profile (autapomorphy)
- moderate superior transverse torus, low rounded inferior transverse torus (autapomorphy)
- upper central and diminutive lateral incisors with strong lingual basal tubercles; upper incisors with flexed roots (could not test roots)
- upper canines with exposed dentin strip along distal edge when worn; apelike maxillary and mandibular canine wear (couldn't determine wear patterns)
- extensive pneumatization of temporal squama (couldn't test as most *Pan paniscus* were casts)
- strong inferomedial inflection of mastoid process (did not test)
- high occipital scale ratio in males and some females (did not test)

The last widely accepted species to be named, *Australopithecus afarensis* was defined by 55 different traits. Of these, 18 or 32%, were capable of separating out the two species of chimpanzee, while 25, or 45%, were not. Autapomorphic traits accounted for 7, or 13%, and when added to the traits capable of separating, we arrive at 45%. The exact same number of traits are capable of separating the chimpanzee species as are not capable. As such, the validity of this species would appear to be in doubt. Resolution may lie in the traits enumerated by the original namer of this taxon as being capable of separating *Australopithecus afarensis* from *Australopithecus africanus* (see section 4.3.12 below).

Table 11. *Australopithecus afarensis* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	11	19
Non-metric data, separate populations	7	13
Metric data, no separation	3	5
Non-metric data, no separation	22	40
Autapomorphic traits	7	13
Non-replicable traits	5	9
Total	55	100

4.3.10 *Australopithecus aethiopicus* Kimbel, White and Johanson

Metric Data - Different Populations

- absolutely large anterior tooth row (size of individual teeth)
- flat cranial base (head balance index)
- nasion coincident with high glabella (g-n length)
- relatively enlarged postcanine tooth row (size of individual teeth)
- strong upper facial prognathism
- short cranial base (basion - inion + basion - foramen ovale)
- flat palate (palate depth at C&I, P^4&M^1, M^2&M^3)

Non-metric Data - Different Populations

- temperomandibular joint flat, open anteriorly
- zygomatic process forward relative to palate length (based on Rak's conclusion)
- anterior vomer insertion coincident with anterior nasal spine
- nasoalveolar contour projects weakly anterior to bicanine line (anterior tooth row curvature); also, incisors in bicanine line (redundant)
- heart shaped foramen magnum
- supraorbitals in form of "costa supraorbitalis"
- guttered nasoalveolar clivus grades into nasal cavity floor

Metric Data - No Separation

- shallow palate (measured between P^4&M^1)
- nasals widest superiorly

Non-metric Data - No Separation

- postglenoid process anterior to tympanic plate
- maxillary dental arch convergent posteriorly
- zygomaticoalveolar crest weakly arched in facial view (sweeping of zygomatic)
- reduced medial inflection of mastoid process (mastoid process shape)
- temporoparietal overlap at asterion
- tympanic vertically deep, with strong vaginal process (WRT post glenoid process)
- mastoid bulbous, inflated beyond supramastoid crest
- receding frontal squama with "trigonum frontale"

Autapomorphic or Non-Replicable traits

- strongly flared parietal mastoid angle (?asterionic notch)
- "dished" midface (autapomorphy)
- extensive temporal squama pneumatization (couldn't test as most of *Pan paniscus* material was casts)
- vertically inclined tympanic plate inferosuperiorly concave (did not measure this trait)
- maxillary lateral incisor roots medial to nasal aperture margins (was unable to test any aspect of root development, size, etc. so as not to damage any skeletal materials)

The newly named *Australopithecus aethiopicus* would appear on the basis of this analysis to be a valid species, as 14, or 48%, of the traits are capable of separating out the two species of chimpanzee. This is compared to the 10, or 35%, of the traits which cannot do so. When the autapomorphies are added to the group, it can be seen that 55% of the traits validly separate out in outgroup analysis. The only remaining question thus becomes whether an entire species should be erected based on only one single skull and a dubious association with an edentulous mandible found a thousand miles away.

Table 12. *Australopithecus aethiopicus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	7	24
Non-metric data, separate populations	7	24
Metric data, no separation	2	7
Non-metric data, no separation	8	28
Autapomorphic traits	2	7
Non-replicable traits	3	10
Total	29	100

4.3.11 *Australopithecus ramidus* White, Suwa and Asfaw

Metric Data - Different Populations

- postcanine dentition significantly smaller than *A. afarensis*
- upper canines larger relative to the postcanine teeth (canine-post canine tooth index)
- lower canines larger relative to the postcanine teeth (canine-post canine tooth index)

Non-metric Data - Different Populations

- upper third premolar more strongly asymmetrical

Metric Data - No Separation

Non-metric Data - No Separation

- temperomandibular joint without definable articular eminence
- lower third premolar more strongly asymmetrical
- lower third premolar with dominant, tall buccal cusp (always for chimps)
- lower third premolar with steep, posterolingually directed transverse crest (always for chimps)
- upper third premolar with relatively larger, taller, more dominant buccal cusp (always for chimps)
- lower dm1 narrow
- lower dm1 obliquely elongate
- lower dm1 with no anterior fovea
- lower dm1 with small and distally placed metaconid
- lower dm1 with large protoconid (mesiobuccal cusp)
- lower dm1 with small, low talonid with minimal cuspule development

Autapomorphic or Non-replicable Traits

- absolutely and relatively thinner canine and molar enamel (couldn't test enamel thickness)

The most recently named hominid fossil species, *Australopithecus ramidus*, was named almost entirely on teeth. Of the 16 traits used to name this new taxon, only 4, or 25%, are capable of separating out the two species of chimpanzee, while fully 69%, 11 of the traits, cannot. This would appear to be the most clear example of an invalid species. Almost all of the traits listed out could not distinguish the two chimpanzee species, despite the fact that mention was made of the closeness *Australopithecus ramidus* bore to these apes. Very few of the traits were diagnostic among the apes, and therefore it is recommended that this species name be suppressed until the true taxonomic affinities of the fossils are better known.

Table 13. *Australopithecus ramidus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	3	19
Non-metric data, separate populations	1	6
Metric data, no separation	0	0
Non-metric data, no separation	11	69
Autapomorphic traits	0	0
Non-replicable traits	1	6
Total	16	100

4.3.12 *Australopithecus africanus* vs. *Australopithecus afarensis*

Metric Data - Different Populations

- dental arcade length
- mandibular ramus breadth
- mandibular ramus height
- mandibular corpus depth (especially anteriorly)
- mandibular incisor region length

- I^1 size
- P^3 larger than P^4
- upper and lower anterior teeth in *A. afarensis*, compared with those of *A. africanus*, are relatively larger when compared with to the posterior dental battery
- *A. afarensis* has the steepest nuchal plane of any hominid, whereas in *A. africanus* it is more horizontal

Non-metric Data - Different Populations
- compound temporal/nuchal crest
- mandibular fossa depth
- *A. afarensis* has a high occipital scale ratio (nuchal plane dominance) in males and some females, a condition similar to apes; it is lower in *A. africanus* and only in males is it high

Metric Data - No Separation
- palate depth
- symphyseal axis angulation
- the anterior mandibular corpus is receding and bulbous in *A. afarensis*; in *A. africanus* it is usually straighter and more vertical (mandibular symphysis angle)
- *A. afarensis* has a very shallow palate, while in *A. africanus* it is deeper
- *A. afarensis* has a flat palate, while in *A. africanus* it shows premaxillary shelving (both chimps show significant premaxillary shelving)

Non-metric Data - No Separation
- naso-alveolar clivus (convex vs. flat or concave)
- dental arcade straight sided/parabolic
- canine jugae size (anterior buttressing)
- articular eminence (weak/strong)
- mastoid process size
- mastoid process shape (rounded/bulbous)
- mandibular canine lingual ridge development
- diastema at I^2/C
- diastema at C/P_3
- the P_3 in *A. afarensis* is usually an asymmetrical oval and is unicuspid in males and females; in *A. africanus* P_3 is rounder in shape and bicuspid
- in *A. afarensis* there is a high frequency of straight or slightly laterally concave mandibular tooth rows; in *A. africanus* they are laterally convex

- the transverse buttress on the face of A. *afarensis* is absent in A. *africanus*
- in A. *afarensis* the snout is characterized by a semi-oval outline due in large part to the convex naso-alveolar clivus; in A. *africanus* the clivus is flatter and straighter
- in basal view the tympanic in A. *afarensis* is tubular and horizontal; in A. *africanus* it is vertical with a strongly curved anterior face (tympanic with respect to postglenoid process)
- in A. *afarensis* the mandibular fossa is shallow owing to a weak articular eminence; in A. *africanus* the eminence is moderate or strong and hence the fossa is deep (articular eminence size)

Autapomorphic or Non-Replicable Traits

- in A. *afarensis* the lateral mandibular surface always bears a shallow depression, posterosuperior to the mental foramen; in A. *africanus* this region is usually swollen. There is some minor overlap, but no A. *afarensis* specimen exhibits the degree of mandibular swelling seen in A. *africanus* and no specimen of A. *africanus* shows the degree of hollowing seen in A. *afarensis* (autapomorphy)
- the asterionic notch of A. *afarensis*, previously known only in apes, is absent in A. *africanus* (symplesiomorphy)
- in A. *afarensis* males the canine fossa is so deep it gives a pinched appearance to the face; in A. *africanus* males it is usually reduced to a narrow groove or is absent (autapomorphy)
- in A. *afarensis* the superior transverse torus is weak to moderate; it is stronger in A. *africanus*
- in A. *afarensis* the extensive pneumatization of the temporal squama is similar to the ape condition; in A. *africanus* temporal pneumatization is more limited to the mastoid region (pneumatization could not be studied)
- upper and lower canines often exhibit pongid-like wear in A. *afarensis*, whereas canine wear is strictly apical in A. *africanus* (wear patterns not studied)
- in more advanced stages of cheek tooth wear the lower canines and third premolars of A. *afarensis* project above the tooth row, while in A. *africanus* all teeth are worn flat (wear patterns not studied)
- in A. *afarensis* the mental foramen is placed low and opens anterosuperiorly; in A. *africanus* it is at mid-corpus height and opens laterally or slightly anteriorly (mental foramen not studied)

Based on this list of 40 traits, it would appear that the case for the separation of *Australopithecus afarensis* and *Australopithecus africanus* is not as strong as some would have it. Of the 40 traits, only 12, or, 30% are capable of differentiating between the two species of chimpanzee, while 20, or 50%, cannot separate. Autapomorphic traits account for 4, or 10%, and added to the separating traits still yield only 40% separation. It would appear that the separation of the two into species requires reconsideration.

Table 14. *Australopithecus afarensis* vs. *Australopithecus africanus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	9	22.5
Non-metric data, separate populations	3	7.5
Metric data, no separation	5	12.5
Non-metric data, no separation	15	37.5
Autapomorphic traits	4	10
Non-replicable traits	4	10
Total	40	100

Beyond the list above, certain alteration may be necessary as well. In 1980, Tobias rebutted Johanson et al. (1978) and Johanson (1980), and went trait for trait on numerous cranial, mandibular and dental features. Most of these features were later used by Johanson (1980; 1985) in his discussion of the validity of the new species. Tobias looked at the exact traits utilized by Johanson, and their ability to separate *Australopithecus afarensis* from other known australopithecine species. The following traits were taken from Johanson et al. (1978), and critically examined. It was found by

Tobias that these traits were not as diagnostic as had been proclaimed.

- "strong alveolar prognathism" - same for many *A. africanus* specimens
- "convex clivus" - same for many *A. africanus* specimens
- "dental arcade long, narrow, straight sided" - same for many *A. africanus* specimens
- "compound temporal/nuchal crest (in larger specimens)" - seen in *A. boisei* as well as possibly in Makapansgat MLD1, plus not in all Hadar specimens - variable development and therefore cannot be used
- "shallow mandibular fossae with weak articular eminences placed only partly under braincase" - these three traits are diagnostic of all australopithecines, and cannot distinguish any from each other
- "ascending ramus of mandible broad, not high" - seen in *A. africanus* specimens
- "moderate superior mandibular transverse torus" - highly variable character found in many A. africanus jaws
- "low rounded inferior mandibular transverse torus" - fits most *A. africanus* mandibles
- "anterior corpus rounded and bulbous" - highly variable trait seen in many *A. africanus* specimens
- "strong posterior angulation of symphyseal axis" - highly variable trait which characterizes most *A. africanus* and *A. robustus* jaws
- "upper central incisors relatively and absolutely large" - measures do not distinguish *A. africanus* and *A. afarensis*
- "diminutive lateral incisors" - *A. africanus* teeth are quite close in size, but in fact are slightly smaller than *A. afarensis*
- "strong variation in canine size" - highly variable trait showing no separation between *A. afarensis* and *A. africanus*
- "canines asymmetric, lowers with strong lingual ridge" - diagnostic feature of *A. africanus*
- "P3 occlusal outline elongate oval in shape w/main axis mesiobuccal to distolingual at 45°-60° to tooth row, dominant buccal cusp, small lingual cusp often expressed only as inflated lingual ridge" - shape described is exactly as seen in Sterkfontein and Makapansgat, therefore no distinction between *A. afarensis* and *A. africanus*

- "postcanine (mandibular) teeth aligned in straight rows" - also found in *A. africanus* therefore not diagnostic

If Tobias is correct, and these traits cannot distinguish between *Australopithecus africanus* and *Australopithecus afarensis*, then they should be removed from consideration as diagnostic. If this is done, the following revised list is achieved:

<u>Metric Data - Different Populations</u>

- mandibular corpus depth (especially anteriorly)
- mandibular incisor region length
- P^3 larger than P^4
- upper and lower anterior teeth in *A. afarensis*, compared with those of *A. africanus*, are relatively larger when compared with to the posterior dental battery
- *A. afarensis* has the steepest nuchal plane of any hominid, whereas in *A. africanus* it is more horizontal

<u>Non-metric Data - Different Populations</u>

- *A. afarensis* has a high occipital scale ratio (nuchal plane dominance) in males and some females, a condition similar to apes; it is lower in *A. africanus* and only in males is it high

<u>Metric Data - No Separation</u>

- palate depth
- *A. afarensis* has a very shallow palate, while in *A. africanus* it is deeper
- *A. afarensis* has a flat palate, while in *A. africanus* it shows premaxillary shelving (both chimps show significant premaxillary shelving)

<u>Non-metric Data - No Separation</u>

- canine jugae size (anterior buttressing)
- mastoid process size
- mastoid process shape (rounded/bulbous)
- mandibular canine lingual ridge development
- diastema at I^2/C
- diastema at C/P_3
- the transverse buttress on the face of *A. afarensis* is absent in *A. africanus*

- in A. *afarensis* the snout is characterized by a semi-oval outline due in large part to the convex naso-alveolar clivus; in A. *africanus* the clivus is flatter and straighter
- in basal view the tympanic in A. *afarensis* is tubular and horizontal; in A. *africanus* it is vertical with a strongly curved anterior face (tympanic with respect to postglenoid process)

Autapomorphic or Non-Replicable Traits

- in A. *afarensis* the lateral mandibular surface always bears a shallow depression, posterosuperior to the mental foramen; in A. *africanus* this region is usually swollen. There is some minor overlap, but no A. *afarensis* specimen exhibits the degree of mandibular swelling seen in A. *africanus* and no specimen of A. *africanus* shows the degree of hollowing seen in A. *afarensis* (autapomorphy)
- the asterionic notch of A. *afarensis*, previously known only in apes, is absent in A. *africanus* (symplesiomorphy)
- in A. *afarensis* males the canine fossa is so deep it gives a pinched appearance to the face; in A. *africanus* males it is usually reduced to a narrow groove or is absent (autapomorphy)
- in A. *afarensis* the extensive pneumatization of the temporal squama is similar to the ape condition; in A. *africanus* temporal pneumatization is more limited to the mastoid region (pneumatization could not be studied)
- upper and lower canines often exhibit pongid-like wear in A. *afarensis*, whereas canine wear is strictly apical in A. *africanus* (wear patterns not studied)
- in more advanced stages of cheek tooth wear the lower canines and third premolars of A. *afarensis* project above the tooth row, while in A. *africanus* all teeth are worn flat (wear patterns not studied)
- in A. *afarensis* the mental foramen is placed low and opens anterosuperiorly; in A. *africanus* it is at mid-corpus height and opens laterally or slightly anteriorly (mental foramen not studied)

When Tobias' alterations are taken into consideration, the following results are achieved. Out of 26 traits, 6, or 24%, separate between chimpanzee species, while 12, or 48%, do not. Adding the autapomorphies to the separating traits, we see that 9, or 36%, of the traits can separate, while again, 48% cannot. Again, we see that the separation between *Australopithecus africanus* and *Australopithecus afarensis* might require some serious rethinking, as it does not appear that they should indeed be considered different species. The majority of the traits which are claimed to be capable of distinguishing the two species are not capable of doing so for the chimpanzees.

Table 15. *Australopithecus afarensis* vs. *Australopithecus africanus* Trait Separation List (modified).

	Number	Percent (%)
Metric data, separate populations	5	20
Non-metric data, separate populations	1	4
Metric data, no separation	3	12
Non-metric data, no separation	9	36
Autapomorphic traits	3	12
Non-replicable traits	4	16
Total	25	100

4.3.13 *Australopithecus robustus* vs. *Australopithecus boisei*

Metric Data - Different Populations

- the size and especially buccolingual diameters of the cheek teeth, which significantly exceed those of *A. robustus*
- greater disparity between canine and premolar size than in *A. robustus*
- elongation of the face as a whole (n-pr)
- elongation of the maxilla (ol-sta)

Non-metric Data - Different Populations

- curiously foreshortened foramen magnum (which may only be an individual variation) (foramen magnum shape)
- more powerful supra-orbital torus

- the earlier or more primitive stage in the trend towards reduction of the cingulum, a stage which the Olduvai cranium shares with *A. africanus*, whereas *A. robustus* represents a more advanced stage of reduction, having only weak vestiges of a lingual cingulum and no trace of the buccal cingulum (maxillary teeth, all cingula included)

Metric Data - No Separation
- marked reduction of the MD diameter of M^3 as compared with that of M^2 and equality of BL diameters of M^3 and M^2, in which the Olduvai specimen resembles *A. africanus* and not *A. robustus* (in which both diameters usually increase from M^2 to M^3)
- elongation of the nose (n-ns)

Non-metric Data - No Separation
- the flexion of the naso-alveolar clivus
- morphology of the zygomatic buttress (transverse buttress)
- nature and extent of the masseteric impressions
- anterior shelving of the palate
- the shape, cusp pattern, Carabelli formation, and buccal cingular vestige of M^3, all of which are nearer to those of *A. africanus*
- morphology of the lingual face of the maxillary canines
- morphology of the malar notch (malar area)

Autapomorphic or Non-Replicable Traits
- absence of even the slightest trace of a canine fossa (autapomorphy)
- the morphology of the labial faces of I^1 and I^2 (autapomorphy)
- morphology of the crowns of M^1 and M^2 (cannot reproduce without more detail as to exact differences)

In his landmark monograph on the OH5 skull, Tobias (1967b) indicated that he believed it to represent a new species, *Australopithecus boisei*. This publication set the tone for hominid fossil taxonomy for the next 10 years, and still today provides the justification for splitting the two taxa. In this publication Tobias listed out 18 traits that he believed separated the two species, which made them valid taxa. Of these 18 traits, 7, or 39%, are capable of separating out the two species of chimpanzee, while 8, or 44%, are not. There are two autapomorphic traits which account for 11% of the total traits, and when added to the separating traits show 50% of the total traits are capable of separating out the two chimpanzee species. Only 1 trait, 6%, was non-replicable owing to difficulty in interpretation. It would therefore appear, based on available evidence, that the two groups are validly differentiated, but that the exact status of the differences might be questioned. It is quite possible that Tobias' (1968) interpretation was actually correct, and that the two represent a superspecies, or a group in the midst of a speciation event.

Table 16. *Australopithecus robustus* vs. *Australopithecus boisei* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	4	22
Non-metric data, separate populations	3	17
Metric data, no separation	2	11
Non-metric data, no separation	6	33
Autapomorphic traits	2	11
Non-replicable traits	1	6
Total	18	100

4.4 Summary

Based on the above analysis of the specific status of the australopithecines, a number of conclusions may be reached (see table 17). For *Australopithecus africanus* it was determined that 49% of the traits listed out were able to separate out the two species of chimpanzee, while 50% were not. This would appear to call into question the validity of the taxon, or at least the traits used to define it. However, since this was the first australopithecine species named, it has precedence, and therefore must stand as the measuring stick for all other taxa.

Australopithecus (Plesianthropus) transvaalensis showed 55% of its traits were not capable of distinguishing between the chimpanzee species, while only 33% were. The sinking of this taxon into *Australopithecus africanus* was fully warranted, both because the traits cannot separate, and because of the extreme paucity of traits listed out for it.

When we look at *Australopithecus robustus*, we note that the majority of the traits, 57%, validly separate out the taxon from all others. Only 42% were not capable of doing so. This appears to be a valid taxon.

Australopithecus prometheus poses something of a problem for this analysis. Fully 57% of its traits were capable of separating the chimpanzee species. It must be remembered however, that only 7 traits were used to define the species, and that the main component of Dart's original description was the fact that he believed he had evidence of the use of fire. The fire aspect has since been disproven, and with it went the main thrust of Dart's distinction. Based on this, and on the paucity of traits listed out for this analysis, the sinking of *Australopithecus prometheus* into *Australopithecus africanus* seems fully justified. This is also the conclusion Grine came to when he stated that "there is little morphological evidence to support a taxonomic distinction among the Taung, Sterkfontein, and Makapansgat (type site *Australopithecus prometheus*) specimens (Grine, 1985:163)." *Australopithecus prometheus* is not a valid taxon.

The taxon *Australopithecus crassidens*, based on this analysis, appears to be an invalid one. Of the traits uncovered defining it, only 33% were able to provide separation, while 67% showed no ability to distinguish between the two species of chimpanzee. Recent efforts by Grine (1981; 1984; 1985) to reintroduce this species are difficult to replicate in this study, owing to the technological sophistication required which is far beyond the scope of this study (including electron micrography). Nonetheless, based on the traits which could be studied it appears that the sinking of *Australopithecus crassidens* into *Australopithecus robustus* was perfectly justified. *Australopithecus crassidens* is not a valid taxon.

The taxon *Telanthropus capensis* provides another of the difficult species in this study in that it again appears to be a valid taxon. Of the traits uncovered defining it, 54% provide separation, while only 23% indicate no separation. It must again be remembered that this species was named based on one single mandible, and that one of its namers, Robinson, subsequently sank it into *Homo erectus*, further reducing the potential validity of this species. A taxon defined entirely on one single mandible must be carefully analyzed, especially in light of the fact that many of the other species covered here are known from hundreds of specimens. This study would seem to contra-indicate the absorption into *Homo erectus*, but the validity of such flimsy evidence must be considered.

The species *Australopithecus boisei* appears to be a valid species based on this analysis, since 51.5% of the traits used to define the species do provide separation of the chimpanzee species. Note must also be made of the fact that as many as 45.5% of the traits were unable to provide separation. While most were able to distinguish the groups, many weren't, possibly indicating a close relationship between this and certain other taxa. The comparison of *robustus* and *boisei* might shed further light on this (see below).

Paraustralopithecus aethiopicus provides again the same dilemma faced with *Telanthropus capensis*. We see here again a species named on one single mandible. Of the traits listed out, 71% are capable of differentiating between the chimpanzees, while 14% are incapable. Nonetheless, few ever accepted the validity of this taxon. There are three possible explanations for this outcome. First, it is possible that a valid taxon is represented. This is not considered likely, as it has never been widely accepted as a valid taxon, and was ignored until 1988 when it was re-erected as a way of accommodating a new fossil find. Second, there is a possible flaw in the methodology employed in this thesis' use of outgroup comparison. The justification for the methodology has been outlined above, and it is believed that this is not the reason. Third, and most likely, is the possibility that the naming of an entire new species (and genus) based on isolated, fragmentary, and very limited fossil remains is inappropriate. The naming of new species on a single mandible would thus appear to be a highly questionable act, and based on the taxa noted in this study, an improper procedure which should be refrained from.

The next species, *Australopithecus afarensis* provides again more difficulty. Exactly 45% of the traits separate the chimpanzee species, and exactly 45% do not provide separation. At the very least, this casts some serious doubts on the validity of the species, and many of the traits used to define it. Further resolution of the problem will be achieved below when the traits used to specifically distinguish between *Australopithecus afarensis* and *Australopithecus africanus* are analyzed.

The taxon *Australopithecus aethiopicus* was named to accommodate the new skull, KNM-WT17000. The authors (Kimbel et al., 1988) apparently believed that the taxon represented by *Paraustralopithecus aethiopicus* was a valid one, as they referred the new skull to the same species, this time housed within *Australopithecus*. The results of this study show that 55% of the traits separate out the chimpanzee species, while 48% do not. This, combined with the above results which showed that *Paraustralopithecus aethiopicus* might in fact be valid lead to the conclusion that this in fact represents a new taxon not before sampled. It is therefore tentatively concluded that *Australopithecus aethiopicus* represents a valid taxon, pending more fossil discoveries.

The latest hominid species to be named, *Australopithecus ramidus*, provides the clearest resolution in this study. Of the traits used to name this new species, only 25% can separate out the chimpanzee species, while as many as 69% cannot. It is quite clear that this taxon was premature, and that it does not appear at all to be a valid taxon.

In the comparison between *Australopithecus afarensis* and *Australopithecus africanus*, it was noted that only 40% of the traits listed were able to differentiate between the species of chimpanzee, while 50% were not able. This would appear to indicate that the two groups should perhaps not be separated, since the majority of the traits said to show such separation in fact, cannot do so. When the list of traits is modified to remove those traits which were said to be able to separate *Australopithecus afarensis* and *Australopithecus africanus* but could not, the results are quite similar. Of the remaining traits, 36% provided separation, but 48% could not. This strengthens the argument that the two taxa are not sufficiently different to require a specific division. Again, the majority of the traits said to be able to separate out the two could not provide any separation in an outgroup comparison.

Finally, the separation of *Australopithecus robustus* and *Australopithecus boisei* appears to be a valid one. As many as 50% of the listed traits separated the chimpanzee species, while 44% could not. The separation between these two groups appears to be valid, with the majority of the traits being capable of distinguishing outgroup comparisons.

Table 17. Separation of Taxa - Summary

Taxon	Traits*		
	Separation†	No Separation	Non-Replicable
Australopithecus africanus	35 (49)	36 (50)	1 (1)
Plesianthropus transvaalensis	3 (33)	5 (55)	1 (11)
Australopithecus robustus	40 (57)	30 (42)	1 (1)
Australopithecus prometheus	4 (57)	0 (0)	3 (43)
Australopithecus crassidens	2 (33)	4 (67)	0 (0)
Telanthropus capensis	7 (54)	3 (23)	3 (23)
Australopithecus boisei	33 (51.5)	29(45.5)	2 (3)
Paraustralopithecus aethiopicus	5 (71)	1 (14)	1 (14)
Australopithecus afarensis	25 (45)	25 (45)	5 (9)
Australopithecus aethiopicus	16 (55)	14 (48)	3 (10)
Australopithecus ramidus	4 (16)	11 (69)	1 (6)
A. africanus vs. *A. afarensis*	16 (40)	20 (50)	4 (10)
A. africanus vs. *A. afarensis* (mod.)	9 (36)	12 (48)	4 (16)
A. robustus vs. *A. boisei*	9 (50)	8 (44)	1 (6)

*total number of traits, percentage in parentheses
†category separation includes autapomorphic traits

Chapter 5 - Trait Separation for *Pan troglodytes* and *Gorilla gorilla*

5.1 Introduction

This chapter will deal with the statistical separation for the generic level. It will utilize the exact same statistical procedures as seen in chapter 4, and the exact same methodology.

The only difference in computation revolved around the use of the Fisher's Exact test. Since the number of gorilla specimens was quite large, there was no problem with small sample sizes for any of the measures testing the generic distinction between *Pan troglodytes* and *Gorilla gorilla.* Therefore, for all gorilla measures, the chi-square value was relied upon for all statistical conclusions.

Data on the gorilla specimens was collected at the same time as for the chimpanzees at the various institutions in the United States, producing the following results:

Table 18. Specimens Utilized in Study.

Cleveland Museum of Natural History

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	12	14	1	10
Gorilla gorilla	5	5	0	6

American Museum of Natural History

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	9	7	0	12
Gorilla gorilla	7	3	0	11

National Museum of Natural History

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	4	4	0	9
Gorilla gorilla	9	10	0	1

Total Chimpanzee Specimens Collected

Juvenile/Adult	Male	Female	Sex Unknown	**Infant**
Pan troglodytes	25	25	1	31
Gorilla gorilla	21	18	0	18

In the case of the gorillas, large enough sample sizes were available to allow for ease of statistical manipulation. In all cases but one, mandibles were associated with the crania. There was one cranium without an associated mandible, and one mandible without an associated cranium. The two were not artificially affiliated.

In total, 39 gorilla specimens were studied, 21 of them male, and 18 of them female. The sex was readily identified on all specimens. There was also a total of 18 infant skulls analyzed.

All statistical manipulations appear in the appendices at the end of this thesis. They are divided into four sections: **Appendix A**) metric data - t-tests performed on all measurements for all species, *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla*; **Appendix B**) non-metric data - chi-square tests performed on all comparisons between *Pan troglodytes* and *Pan paniscus*; **Appendix C**) non-metric data - chi-square tests performed on all comparisons between *Pan troglodytes* and *Gorilla gorilla*; **Appendix D**) tables of all raw data.

5.2 Trait Separation

For a fuller discussion of the statistical manipulations and methodology employed in this chapter, please refer to chapter 4.

5.2.1 *Australopithecus* Dart

Metric Data - Different Populations

- symphyseal surface relatively straight and approaching the vertical
- progressive increase in size of permanent lower molars from first to third
- massive jaws, especially in the robustness of the corpus, but varying considerably in absolute size (mandibular size index; also index of robusticity)
- ascending mandibular ramus usually sloping backward (mandibular angle)
- ascending mandibular ramus of moderate height
- moderately large anterior dentition
- prognathic face
- canines large
- forehead present (supra-orbital height index)
- zygomatic arch moderately developed (bi-zygomatic breadth index - Rak)
- temporal fossa of medium size (temporal foramen - Rak)
- palate of more or less even depth (one sided t-test palate depth)
- tooth row compact (premolar and molar tooth row length)
- mandibular anterior and postcanine teeth harmoniously proportioned (Canine to post-canine teeth indices)
- moderate to fairly high orbits, with a lower mean height than in pongids
- foramen magnum well forward on the base of the cranium (head balance index; basion - foramen ovale)
- inion low and generally close to the Frankfurt Horizontal plane (basion-inion; also, extreme largeness of male gorilla nuchal crests makes inion highly variable point)
- porion elevated in position above the nasion-opisthion line (auricular height: porion - bregma)
- relatively large premolars

- relatively large molars, the enlargement being more marked in the buccolingual diameter of the crown
- relatively small cranial capacity, with an average about 500 c.c. and an estimated population range of 360 to about 640 c.c.; endocranial volume of the order of 450-550cc

<u>Non-metric Data - Different Populations</u>

- tendency in larger individuals to form low sagittal crest in frontoparietal region of the vertex of the skull
- consistent development of a pyramidal mastoid process typical of hominid form and relationships
- mandibular fossa constructed on the hominid pattern but in some individuals showing a pronounced development of the postglenoid process
- relatively large premolars and molars
- weakly to moderately developed supraorbital torus
- heavily pneumatized cranial base
- vomer does not insert directly against back of anterior nasal spine
- distinction between floor of nasal cavity and subnasal maxillary surface present but poor
- sagittal crest is not continuous with either the nuchal crest or the occipital torus, whichever is present
- contour of internal mandibular arch V-shaped or blunt U-shaped
- no diastema
- occipital condyles well behind the anteroposterior midpoint of the cranial length, but in the same coronal plane as the external acoustic apertures
- planum nuchale of occipital bone rising only a short distance above the Frankfurt Horizontal and generally facing downwards much more than backwards (Gorilla male nuchal plane always greatly expanded and facing backwards)
- low nuchal crest
- a mandibular fossa which is shallow and mediolaterally broad

<u>Metric Data - No Separation</u>

- distinct sexual dimorphism in canine size (both gorillas and chimps show this dimorphism)
- large face (Rak's facial indices)
- skull narrow (eu-eu)
- maxillary anterior and postcanine teeth harmoniously proportioned (Canine to post-canine teeth indices)
- robust jaws (mandibular index of robusticity)

- mandibles showing marked individual variation in respect of absolute size (CoV for mandible size 6.9% for chimpanzees, 8.7% for gorilla - both acceptable levels of individual variation)
- M^3 is commonly smaller than M^2

Non-metric Data - No Separation

- an anterior position of the zygomatic process of the maxilla with the anterior root of the zygoma arising between C and M1 (and the consequent appearance of facial flattening)
- tendency for the appearance of a frontal trigone
- 1st deciduous molar differs markedly in the shape of the cusps
- 1st deciduous molar differs markedly in the arrangement of the cusps
- lower deciduous 1st molar incompletely molarized; pronounced molarization of the lower 1st deciduous molar
- lower deciduous 1st molar protoconid most strongly developed cusp (incl. anterior accessory cusplet) with large sloping buccal surface
- dm_1 anterior fovea displaced lingualward and open to that side
- mandibular canine strongly asymmetrical
- mandibular canine lingual ridge present, normally strongly developed
- maxillary incisor and canine sockets in parabolic curve
- cranium with marked pneumatization
- lower anterior premolar with subequal cusps (ape lower 3rd premolars always possessed subequal cusps)

Autapomorphic or Non-Replicable Traits

- dental arcade parabolic in form with no diastema (autapomorphy)
- widely flared zygomatics (autapomorphy)
- mental eminence absent or slightly indicated (mental eminence is an autapomorphy for hominids)
- 2nd deciduous molar longer and narrower (did not test)
- 2nd deciduous molar differs in arrangement of cusps (did not test)
- a relatively thin walled cranium rendered robust in parts by strong ectocranial superstructures (cranial thickness could not be tested; ectocranial superstructures include the sagittal, nuchal, and occipito-mastoid crests, tested above)
- P3 usually having a single buccal root (could not test root development)
- endocasts distinguished from pongids by a posterior placement of the lunate sulcus (no test of cranial endocasts)

- massive post-canine dentition relative to body size (no test of body size performed)
- spatulate canines wearing down flat from the tip only (couldn't test dental wear)

When the genus *Australopithecus* is tested, it can be noted that of the 65 total traits used to define the genus, 36, or 55%, provide separation between *Gorilla* and *Pan*. Only 19 traits, or 29%, do not provide separation. When the 3 autapomorphic traits are added to the list of those which validly separate the genera, we get a total of 39, or 60%, providing separation. These numbers show the genus *Australopithecus* to be quite valid, based on numerous acceptable morphological characteristics. It should also be noted that 7 traits, totaling 11%, were non-replicable owing to the research design of this thesis.

Table 19. *Australopithecus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	21	32
Non-metric data, separate populations	15	23
Metric data, no separation	7	11
Non-metric data, no separation	12	18
Autapomorphic traits	3	5
Non-replicable traits	7	11
Total	65	100

5.2.2 *Plesianthropus* Broom

The genus *Plesianthropus* was erected based on some extremely flimsy evidence of a single mandible. Basically, Broom felt that certain small features were enough to define a new genus.

- the imperfect lower first milk molar of Sterkfontein so different from the same tooth of *Australopithecus*, they must be generically distinct

No real criteria beyond this were given justifying the creation of this genus, and therefore it is virtually impossible to test the validity of the genus. In the Transvaal Museum Memoirs entitled *Sterkfontein Ape-Man Plesianthropus*, Broom and Robinson go to great pains to prove the hominid affinities of the genus. The only comparisons made are with apes, monkeys, and modern humans. Little mention is made of relations to the other fossil hominid species of the time. Therefore no testing was performed upon this genus, and it is assumed that the sinking of *Plesianthropus* by Robinson (1954) was perfectly justified.

5.2.3 *Paranthropus* Broom

Metric Data - Different Populations

- canines small
- bony face quite flat
- zygomatic arch strongly developed (bi-zygomatic index)
- temporal fossa large (temporal foramen index)
- palate appreciably deeper posteriorly than anteriorly (palate depth one-sided t-test)
- ascending ramus vertical (mandibular angle)
- ascending ramus high
- tooth row compact (premolar and molar tooth row length)
- mandibular anterior teeth very small compared to postcanine teeth (canine to postcanine teeth indices)
- formation of a slightly concave, low forehead (supra-orbital index)
- great enlargement of premolars relative to molars and canines (summed tooth area index)
- anterior teeth small when compared to premolars and molars (summed tooth area index)

- great enlargement of molars and massiveness of tooth-bearing bone (molar row tooth area)
- endocranial volume of 450-550cc

Non-metric Data - Different Populations
- vomer does insert against back of anterior nasal spine
- supraorbital torus well developed near midline (supra-orbital torus development; medial descent)
- distinction between floor of nasal cavity and subnasal maxillary surface totally absent
- sagittal crest normally present in both sexes; great increase in the size of the masticatory musculature and attachments relative to the size of the skull
- internal mandibular arch contour V-shaped
- tooth row without diastema
- presence of a flattened 'rib' of bone across each supra-orbital margin (supra-orbital torus development)
- a glabella that is situated at a lower level than the supra-orbital margin
- naso-alveolar clivus sloping smoothly into the floor of the nasal cavity

Metric Data - No Separation
- skull broad across ear region (eu-eu)
- maxillary anterior teeth very small compared to postcanine teeth (canine to postcanine teeth indices)

Non-metric Data - No Separation
- dm_1 strongly molarized
- metaconid and hypoconid largest cusps, protoconid without large, sloping face
- mandibular canine not strongly asymmetrical
- mandibular canine lingual ridge never strongly developed
- dm_1 with anterior fovea centrally situated and with complete margin
- maxillary canine and incisor sockets in almost straight line across front of palate
- frontal trigone delimited laterally by posteriorly-converging temporal crests
- virtually completely molarized dm_1
- formation on the naso-alveolar clivus of prominent ridges marking the central incisor sockets, but concavities marking the

lateral incisor sockets (all apes showed ridges marking the incisor sockets)

- milk teeth of Kromdraai so different from Taungs, they must belong to different genus (that is all the justification given) (in virtually all respects, the deciduous teeth do not separate between *Pan* and *Gorilla*)

Autapomorphic or Non-Replicable Traits

- formation of a central facial hollow associated with a completely flat nasal skeleton, and a cheek region that is situated anterior to the plane of the pyriform aperture; bony face actually dished (autapomorphy)
- formation of a broad gutter on the superior surface of the posterior root of the zygoma (autapomorphy)
- formation of either a marked pit or a groove across the zygomaticomaxillary suture of the cheek region - at least in South African *Paranthropus* (autapomorphy)
- P3 usually with double buccal roots i.e. three roots all together (roots could not be tested)
- canine small and wears down from the tip (could not test dental wear)
- small incisive canals that open into the horizontal surface of the nasal floor (did not test incisive canals)
- formation of flat occlusal wear surfaces to the cheek teeth, accompanied by smoothly rounded borders between the occlusal surfaces and sides of the crowns of the cheek teeth (wear patterns not studied)

The genus *Paranthropus* was considered to have been effectively sunk in 1964 by Leakey et al. Despite this, it is currently undergoing a resurgence in popularity, with many authors accepting it as representing a valid genus apart from *Australopithecus*. This study has provided some support for this contention. Of the 42 total traits used to define the genus, 23, or 54%, were able to differentiate between *Gorilla* and *Pan*, while 12, or 29%, were unable to do so. If the 3 autapomorphic traits, representing 7% of the traits are added to the separating list, the total becomes 26, or 61%, of the traits listed out which were able to separate out the two outgroup ape genera. There were also 4 traits, or 10%, which were non-replicable owing to research design. This evidence appears to indicate that the genus *Paranthropus* may be defined on traits which are valid and capable of distinguishing it from all other hominid genera. It provides tentative evidence that the genus is in fact a valid one.

Table 20. *Paranthropus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	14	33
Non-metric data, separate populations	9	21
Metric data, no separation	2	5
Non-metric data, no separation	10	24
Autapomorphic traits	3	7
Non-replicable traits	4	10
Total	42	100

5.2.4 Zinjanthropus Leakey

Metric Data - Different Populations

- inion set lower than in *Australopithecus* and *Paranthropus* (despite great muscularity) in Frankfurt horizontal (basion-inion)
- foramen magnum has more horizontal position than in *Australopithecus* (no equivalent structure preserved in any *Paranthropus* samples) (head balance index)
- very unusual position of the nasion, which on the most anterior part of the skull, instead of being behind and below glabella
- very deep palate more like *Homo* than is *Australopithecus*, and quite unlike the form seen in *Paranthropus*
- relatively greater reduction of mandibular canines in comparison with the molar/premolar series than is seen in *Paranthropus*

Non-metric Data - Different Populations

- in males the nuchal crest is developed as a continual ridge across the occipital bone
- foramen magnum less elongate than in *Australopithecus* (no equivalent structure preserved in any *Paranthropus* samples)
- mastoids are more similar to those seen in present day man in shape
- presence of a very massive horizontal ridge or torus above the mastoids (much more marked than normal type of supra-mastoid crest)
- mastoids are more similar to those seen in present day man in size
- very great pneumatosis of the whole of the mastoid region of the temporal bones, which even invades the squamosal elements
- very great absolute and also relative width of the inter-orbital area
- the whole shape and position of the external orbital angle elements of the frontal bone (supra-orbital torus follows orbits shape; arched orbits)
- the conformation of the malar-maxillary area of the cheek; in *Australopithecus* and *Paranthropus* there is a buttress of bone from malar to alveolar region near 4th premolar - this buttress absent in Zinj (transverse buttress development)
- presence of a strong wide shelf above the external auditory meatus, posterior to the jugal element of the temporal bone (supra-mastoid crest)

Metric Data - No Separation

- nasal bones are much wider at the top than at their inferior margin
- relatively greater reduction of maxillary canines in comparison with the molar premolar series than is seen in *Paranthropus*

Non-metric Data - No Separation

- very great area of muscle attachment on the inferior margin of the malars

Autapomorphic or Non-Replicable Traits

- very prominent and keeled anterior margin of the crest on the frontal bone for the anterior segment of the temporal muscles in the region of the post-orbital constriction (even most muscular male *Paranthropus* shows nothing comparable) (autapomorphy)

- posterior wall of the occipital bone rises more steeply to form, within the parietals, a very high vaulted posterior region of the skull (autapomorphy)
- the way in which the parietals rise almost vertically behind the squamous elements of the temporal before bending over to become a dome (autapomorphy)
- the shape and from of the tympanic plate, whether seen in norma lateralis or in norma basilis (difference not specified)
- the massiveness of the jugal element of the temporal bone relative to the total size of the temporal bone (did not test)
- relative thinness of the parietals in comparison with the occipitals and temporals (could not test cranial thickness)

Based on this analysis, it would appear that *Zinjanthropus* might represent a valid genus. Of the total 24 traits Leakey (1959) used to define his new genus, 15, or 63%, are capable of separating *Gorilla* from *Pan*, while only 3 traits, 12% are not. There were also 3 non-replicable traits, and 3 autapomorphies, representing 12.5% each. When the autapomorphies are added to those traits which separate, we find that 75.5% of the traits, 18 traits in all, are valid for separation. Unfortunately, these numbers are misleading, as it was soon proven that many of the traits Leakey (1959) used to define his new species were actually not exclusive to that genus.

Table 21. *Zinjanthropus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	5	21
Non-metric data, separate populations	10	42
Metric data, no separation	2	8
Non-metric data, no separation	1	4
Autapomorphic traits	3	12.5
Non-replicable traits	3	12.5
Total	24	100

Almost immediately Robinson took issue with the new genus, and argued trait for trait against 'Zinj'. These are the traits he highlighted:

- inion lower relative to Frankfurt horizontal: it is in fact similar to both *Australopithecus* and *Paranthropus*, almost exactly in the Frankfurt plane
- posterior of occipital forms high vault: similar to *Paranthropus*, less so in *Australopithecus*
- *Paranthropus* has an almost spheroidal brain case which is relatively low and narrow anteriorly, but steep-sided and higher posteriorly - Zinj is similar to this
- *Australopithecus* has a brain-case more similar to dolichocephalic modern hominine
- nasion almost coinciding with glabella: this is true in *Paranthropus* and in some cases of *Australopithecus* ; in *Paranthropus* and Zinj, nasals are relatively very wide near the nasion
- very great absolute and relative width of inter-orbital area: cannot be separated from *Australopithecus, Paranthropus,* or *Homo*, therefore not taxonomic valence
- very deep palate: in *Paranthropus* and Zinj the palate slopes (difference between anterior and posterior depths) with more depth posterior; different from *Australopithecus* and *Homo*
- zygomatic process of maxilla: Zinj has poorly developed zygomatic, similar to that seen in South African specimens
- greater reduction of canines compared to premolars and molars: falls within *Paranthropus* range for a ratio of modules of premolars and molars
- sagittal crest occupies exact same position as *Paranthropus* in Zinj - roughly the middle third of the distance between inion and glabella
- anterior teeth set along straight line across the front of the palate very reduced, while post-canines appreciably larger
- Zinj clearly fits well within *Paranthropus* range, as a slightly more robust type of animal; though not out of the range of other primates
- proposes that Zinj be called *Paranthropus boisei*

If these traits are removed from the definition of *Zinjanthropus*, the following revised list remains:

Metric Data - Different Populations

- foramen magnum has more horizontal position than in *Australopithecus* (no equivalent structure preserved in any *Paranthropus* samples) (head balance index)

Non-metric Data - Different Populations

- in males the nuchal crest is developed as a continual ridge across the occipital bone
- mastoids are more similar to those seen in present day man in shape
- presence of a very massive horizontal ridge or torus above the mastoids (much more marked than normal type of supra-mastoid crest)
- mastoids are more similar to those seen in present day man in size
- very great pneumatosis of the whole of the mastoid region of the temporal bones, which even invades the squamosal elements
- the whole shape and position of the external orbital angle elements of the frontal bone (supra-orbital torus follows orbits shape; arched orbits)
- the conformation of the malar-maxillary area of the cheek; in *Australopithecus* and *Paranthropus* there is a buttress of bone from malar to alveolar region near 4th premolar - this buttress absent in Zinj (transverse buttress development)

Metric Data - No Separation

- nasal bones are much wider at the top than at their inferior margin

Non-metric Data - No Separation

- very great area of muscle attachment on the inferior margin of the malars

Autapomorphic or Non-Replicable Traits

- the shape and from of the tympanic plate, whether seen in norma lateralis or in norma basilis (difference not specified)
- the massiveness of the jugal element of the temporal bone relative to the total size of the temporal bone (did not test)
- relative thinness of the parietals in comparison with the occipitals and temporals (could not test cranial thickness)

We can see that the definition of *Zinjanthropus* becomes much reduced. Although the majority of the traits still separate out the genera of apes, they do so because a total of 11 traits are all that remain of the genus' original description. It would be very difficult to defend a genus based on only 11 traits, 4 of which do not provide any separation at all. Only 7 traits remain to define a genus, and it would seem from this that the sinking of *Zinjanthropus* was in fact quite justified (it must be remembered that the genus was formally sunk by its namer in 1964, Leakey et al.).

Table 22. *Zinjanthropus* Trait Separation List - modified.

	Number	Percent (%)
Metric data, separate populations	1	9
Non-metric data, separate populations	7	64
Metric data, no separation	1	9
Non-metric data, no separation	1	9
Autapomorphic traits	0	0
Non-replicable traits	1	9
Total	11	100

5.2.5 *Ardipithecus* White, Suwa and Asfaw

Metric Data - Different Populations
- lower canines larger relative to the postcanine teeth (C-postC tooth index)
- lower dm1 narrow
- lower dm1 obliquely elongate

Non-metric Data - Different Populations
- temperomandibular joint without definable articular eminence
- lower third premolar more strongly asymmetrical
- lower dm1 with small and distally placed metaconid

Metric Data - No Separation

- upper canines larger relative to the postcanine teeth (C-postC tooth index)

Non-metric Data - No Separation

- upper third premolar more strongly asymmetrical
- lower third premolar with dominant, tall buccal cusp (always for chimps)
- lower third premolar with steep, posterolingually directed transverse crest (always for chimps)
- upper third premolar with relatively larger, taller, more dominant buccal cusp (always for chimps)
- lower dm1 with large protoconid (mesiobuccal cusp)
- lower dm1 with small, low talonid
- lower dm1 with minimal cuspule development
- lower dm1 with no anterior fovea

Autapomorphic or Non-Replicable Traits

- absolutely and relatively thinner canine and molar enamel (couldn't test enamel thickness)

The most recent hominid genus to be named, *Ardipithecus*, does not appear to be a valid genus, based on this study. Of the 16 traits used to define the genus, only 6, or 38%, were capable of separating out the genera of apes, while 9 of the traits, or 56%, were not capable of doing so. This evidence bears even more weight when it is considered that the exact same traits used here were also used to define the species *ramidus*. The species *ramidus* failed to separate, with 69% of its traits being invalid. Here we see that the exact same traits again fail to separate, even though by virtue of the research design of this study, a wider morphological gap was introduced when *Gorilla gorilla* was compared to *Pan troglodytes*, rather than the morphologically much more similar *Pan paniscus*. Essentially, the criteria of the study were relaxed, and even so the new genus failed to prove itself valid. The genus *Ardipithecus*, as well as the species *ramidus*, should be considered *nomina nudum*.

Table 23. *Ardipithecus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	3	19
Non-metric data, separate populations	3	19
Metric data, no separation	1	6
Non-metric data, no separation	8	50
Autapomorphic traits	0	0
Non-replicable traits	1	6
Total	16	100

5.2.6 *Australopithecus/Plesianthropus* vs. *Paranthropus* or 'Gracile" vs. 'Robust'

Metric Data - Different Populations

- facial prognathism usually more marked in *Australopithecus* than in *Paranthropus*
- in *Plesianthropus* the foramen magnum is farther back than in *Paranthropus* (measure distance from foramen magnum to foramen ovale)
- *Paranthropus* has small canines (upper and lower); in *Australopithecus* the canines are larger
- incisors appear to be much smaller in *Paranthropus* than in *Plesianthropus*, both upper and lower
- mandibular premolars (P_3 and P_4) of *Paranthropus* are much larger than *Plesianthropus*
- *Paranthropus* has upper premolars (P^3 and P^4) which are appreciably larger than *Australopithecus*
- *Australopithecus* maxillary molars smaller than *Paranthropus*
- *Australopithecus* mandibular molars smaller than *Paranthropus*
- lower deciduous molar in *Australopithecus* smaller than *Paranthropus*
- *Australopithecus* has an unmistakable forehead; *Paranthropus* has no real forehead (supra-orbital index)
- in *Paranthropus* mandible, molar size increases $M1<M2<M3$, while in *Australopithecus* $M1<M2>M3$
- ramus is low in height

- glenoid well above the occlusal plane (=ramus height of mandible - corpus height)
- brain of *Paranthropus* is very appreciably larger than *Plesianthropus*
- low frontal arch region (supra-orbital index)

Non-metric Data - Different Populations

- *Paranthropus* has maxillary canines with asymmetrical crown; in *Australopithecus* the canines are more symmetrical
- in *Paranthropus* the vomer inserts into the back of the anterior nasal spine, in *Australopithecus* it does not
- sharp demarcation between maxilla and pyriform aperture in *Australopithecus*; demarcation in *Paranthropus*, but not as marked (divide, but not a sill)
- *Australopithecus* has a weakly developed supra-orbital torus; *Paranthropus* has a well developed supra-orbital torus
- in *Australopithecus* the talonid of P^4 is never well developed, while in *Paranthropus* a distinct distal buccal cusp (=talonid) is present (number of cusps)
- *Paranthropus* P_3 more rounded, less asymmetrical; *Australopithecus* P_3 asymmetrical
- deciduous lower 1st molar mesial cuspule present in *Australopithecus*, not in *Paranthropus*
- ramus with wide open sigmoid notch
- endocoronoid buttress passes directly toward the coronoid tip
- powerful jugal arch
- protuberant mastoid region
- P^3 buccal grooves lightly developed in *Paranthropus* , but well defined in *Australopithecus* (cusps separated or united)

Metric Data - No Separation

- in *Australopithecus* the skull is narrow; in *Paranthropus* the skull is slightly larger and broad across the ear region (eu-eu)
- modest sized cheek teeth, and substantial anterior teeth (maxillary)
- relatively great post-orbital constriction

Non-metric Data - No Separation

- *Plesianthropus* no anterior pillars; *Paranthropus: bony* ridge from infra-orbital foramen to front socket of the canine (anterior pillar)
- *Plesianthropus* the large outer cusp of the 2nd lower premolar is completely united with the small posterior

- first upper molars in *Plesianthropus*, the crown is almost square with rounded corners; first upper molars in *Paranthropus*, the crown is rhomboidal
- second upper molars are similar, but *Paranthropus* are more rhomboidal
- *Paranthropus* has mandibular canines with asymmetrical crown; in *Australopithecus* the canines are more symmetrical
- third upper molars: the postero-internal cusp (hypocone) in *Plesianthropus* is large (forming a third of the crown), while in *Paranthropus* it is small (less than a quarter of the crown)
- third lower molars between the two there is considerable agreement, though in *Plesianthropus* the indications of the inner cingulum are more marked than in *Paranthropus* (though only one *Paranthropus* tooth to compare existed at the time)
- in *Australopithecus* the lower deciduous molar has 5 cusps, though hypoconulid is small; in *Paranthropus* the tooth is fully molariform with 5 well developed cusps of equal size (degree molarization)
- in *Australopithecus* the entoconid of lower deciduous molar is a small cusp well separated from the protoconid (protoconid and metaconid separation)
- deciduous lower 1st molar has well developed anterior fovea in *Australopithecus*, displaced lingualward; smaller anterior fovea in *Paranthropus*, centrally placed
- in *Australopithecus* a very strong lingual ridge present in mandibular canine
- maxillary bicanine line in *Australopithecus* curved, while in *Paranthropus* straight
- maxillary incisors very similar in all euhominids as well as prehominids
- *Paranthropus* P_3 has a less well defined lingual cusp; *Australopithecus* P_3 has well developed lingual cusp
- *Paranthropus* molars nearly oval in shape, while *Australopithecus* more rectangular
- deciduous lower 1st molar talonid small in *Australopithecus*, talonid cusps poorly developed; *Paranthropus* with large talonid with well developed cusps
- mandible v-shaped, not u-shaped as in later hominids
- mandibular canine lingual ridge present, normally strongly developed/ never strongly developed
- dm1 protoconid (mesiobuccal) most strongly developed cusp (incl. anterior accessory cusplet) with large sloping buccal

surface/dm1 protoconid without large, sloping face/dm1 metaconid and hypoconid largest cusps
- pneumatized mastoid region
- canines of *Australopithecus* with a well defined apex; not so in *Paranthropus* (canines of all apes are apexed)
- *Plesianthropus* : P_4 main inner cusp is deeply cut into behind by the continuation forwards of the posterior foveal groove; this does not occur in *Paranthropus* (all apes show separation of cusps)

Autapomorphic or Non-Replicable Traits
- *Paranthropus*: the antero-external cusp of 2nd lower premolar is cut off from the small postero-external by a furrow which, on the outer side of the tooth, forms a marked groove (autapomorphy)
- *Paranthropus*: infraorbital portion of the face is nearly flat; the cheeks are as far forward as the nose ('dished' face -autapomorphy)
- dished face (autapomorphy)
- roots of P^3 double in *Paranthropus*, but single in *Australopithecus*; P3 usually having a single buccal root (no test for roots performed)

There were 56 traits which were listed out as proving the genus *Paranthropus* was significantly different from *Australopithecus/Plesianthropus* to warrant such a taxonomic distinction. Of these 56 traits, 27, or 48%, were capable of separating *Gorilla* from *Pan*, while 25 traits, or 44.5%, were not capable of doing so. There were also 3 autapomorphic traits, accounting for 5.5% of the total, as well as 1 non-replicable trait which meant 2% of the total traits. Combining the autapomorphies with the separating traits, we find that 30, or 53.5%, of the traits are able to distinguish between the outgroup apes. This would appear to provide support for the contention that the genus *Paranthropus* is a valid genus, separate from *Australopithecus*. The majority of the traits used to define it, as well as the majority of the traits listed out as separating it from

Australopithecus, support the conclusion that there is a decided morphological gap between these genera.

Table 24. *Australopithecus/Plesianthropus vs. Paranthropus* Trait Separation List.

	Number	Percent (%)
Metric data, separate populations	15	27
Non-metric data, separate populations	12	21
Metric data, no separation	3	5.5
Non-metric data, no separation	22	39
Autapomorphic traits	3	5.5
Non-replicable traits	1	2
Total	56	100

5.3 Summary

The taxonomic status of the genera of the australopithecines can be summarized as such. The genus *Australopithecus*, with 60% of its traits separating, and only 29% not, appears to be a valid genus. The majority of its traits can distinguish between *Gorilla* and *Pan*, and as such are acceptable as defining criteria.

Paranthropus too appears to represent a valid genus, again with the majority of its traits (61%) separating, while only a minority (29%) cannot. This adds strength too the arguments that *Paranthropus* should be re-erected to house the 'robust' material from East and South Africa.

Zinjanthropus is troublesome in that despite being considered an invalid genus for many years by virtually all, it does appear to separate out well. Although it is again possible that it is either a valid genus, or that there is a flaw in the methodology of this thesis, the explanation may again lie in the paucity of fossil material upon which the genus was based. *Zinjanthropus* housed one and only one specimen in its lifetime, the OH5 skull. When the traits used to define the genus are pared down to exclude invalid traits (as did Robinson, 1960), we are left with only 11 traits to define a biologically valid genus, a difficult position to defend. It is concluded here that the genus *Zinjanthropus* was justifiably sunk by Leakey et al. (1964), as was confirmed by Tobias (1967b).

The newly named genus *Ardipithecus* does not appear to represent a valid taxon, as only 38% of its traits provide separation, contrasted to 56% which do not. The majority of the traits argue against it being a biologically valid taxon separate from all other hominid taxa.

Table 25. Separation of Taxa - Summary

Taxon	Traits*		
	Separation†	No Separation	Non-Replicable
Australopithecus	39 (60)	19 (29)	7 (11)
Paranthropus	26 (61)	12 (29)	4 (10)
Zinjanthropus	18 (75.5)	3 (12)	3 (12.5)
Zinjanthropus (modified)	8 (73)	2 (18)	1 (9)
Ardipithecus	6 (38)	9 (56)	1 (6)
'Robust' vs. 'Gracile'	30 (53.5)	25 (45.5)	1 (2)

*total number of traits, percentage in parentheses
†category separation includes autapomorphic traits

Chapter 6 - Summary and Conclusions

6.1 Introduction

For many years it has been apparent that the taxonomy of the australopithecines has been in need of a major re-evaluation. The traits used in the past to define new species have rarely been tested for taxonomic validity, for their actual ability to separate out other closely related species. This failing in paleoanthropology was noted as early as 1965, and the conclusion was reached that "in order to establish a valid species it should be necessary to show characters in the available fossil material which purport to be of the same magnitude as those which separate related living species (Simons and Pilbeam, 1965:101)."

This was the challenge undertaken by this thesis, to determine whether the characters used to define the fossil species of the australopithecines were of the same magnitude as those which separate out modern apes. Traits used in the past to delineate fossil hominid species were compiled into lists, and tested to determine whether or not they could distinguish between chimpanzees and gorillas.

The extremes of taxonomic overindulgence that have plagued the field of human paleontology were uncovered and subjected to closer scrutiny in an attempt to alleviate this problem. It has been noted that "in comparison with other zoological fields, physical anthropology leans heavily upon the genus to distinguish its finds, and one might even say that, allowing for a clearly excessive synonymy, the anthropological genus is more or less equivalent to the zoological species (Brown, 1958:151)." Many outside the field of paleoanthropology feel that the taxonomy is much overburdened. The problem is not restricted to historical considerations, as the recent spate of new hominid taxa clearly shows.

Large influxes of new fossil finds appear to cause the creation of numerous unnecessary names, names which more often than not belong within other already known taxa. Reassessments of these new fossil finds tends to introduce a sobering effect on the field, as noted by Hooton when he stated that "a dispassionate interpretation of new fossil evidence is usually obtainable only when one awaits the reworking of the material by persons not emotionally identified with the specimen (1938:114)." The fame and funding attached to new hominid fossil species can be quite tempting.

It was noted above that there have been three general trends in paleoanthropology relating to new hominid discoveries. In the period from 1925 until approximately 1953, many new species and genera were being named, usually based on meager evidence. Dispassionate reassessments resulted in the sinking of most of these taxa, and in the period from 1953 until about 1978 only one new species was accepted (though not unanimously), and not without a major fight. Subsequent to 1978, we have experienced a large influx of new fossils from such places as Ethiopia, Kenya, and Tanzania. These new fossils have had much the same effect as previous discoveries. They have produced an abundance of new hominid fossil species, most of which appear to be of dubious value. It would appear that a sober reassessment of the hominid taxa by those not emotionally involved with the fossils is overdue.

The existence of excessive fossil species tends to confuse the real evolutionary relationships of the hominids, and draws energy and effort away from what may otherwise be important and informative areas of research. This was noted years ago when the statement was made that "it will not be possible for scholars in this field to devote their principle energies to the recovery of new scientific data as long as their attention is drawn away into the refutation of weakly founded names and the insubstantial deductions which surround their formulation (Simons, 1969:22)." This statement is as true today as it was over 25 years ago.

6.2 Conclusions - Species Level

The species *Australopithecus africanus*, when subjected to this analysis, fared rather poorly. It must be concluded that at least half of the traits used to define this species were poorly chosen, as they could not separate out species of modern chimpanzee. At the very least this must caution paleoanthropologists to choose their character traits with extreme care. Although 50% of the traits used to define this species were invalid, it must still be accepted as a valid species. It was the first one named, and as such is the yardstick by which all others must be measured. There still exists a list of 35 traits which are taxonomically valid for separating out this taxon, which lends a good deal of credibility to the actual species.

Australopithecus (Plesianthropus) transvaalensis showed that 55% of its traits were not capable of distinguishing between the chimpanzee species, while only 33% were. The sinking of this taxon into *Australopithecus africanus* was fully warranted, both because the traits cannot separate, and because of the extreme paucity of traits listed out for it.

When we look at *Australopithecus robustus*, we note that the majority of the traits, 57%, validly separate out the taxon from all others. Only 42% were not capable of doing so. *Australopithecus robustus* was the first of the 'robust' species to be named, and its validity has been well proven by this study. It is concluded that it is a good species, distinguishable from all others by a list of 40 traits which were capable of distinguishing between modern ape taxa.

The taxon *Australopithecus prometheus* was originally named for a single occipital fragment found at Makapansgat by Dart. Dart believed he had found the earliest evidence of fire, and because of this, named a new species of australopithecine. It was later proven that the evidence of fire was misleading, and as a result, the most significant aspect of the new species was removed. Dart had named this new species based mainly on presumed behavioral evidence, providing little by way of morphological grounding. All of the traits used to define the species morphologically revolved around the basal portion of the occipital bone, which could likely be reduced to one single morphological complex. Although the features listed out by Dart appear to separate out this species, when reduced to this one complex, it does not appear to be a valid species. With the behavioral evidence refuted, the minimal morphological evidence is not enough to warrant a new species, and therefore it is concluded that this is not a valid species.

The majority of the traits used to define the species *Australopithecus crassidens* were not able to separate out the species of chimpanzee, and as such, this is considered to be an invalid species. This conclusion can be coupled with the fact that the species was sunk in 1954, and only two authors have ever advocated its resurrection.

Telanthropus capensis was originally named based on one single mandible, and consisted of a total of 13 traits. Of these, 7 provide separation. Again, however, if we reduce the traits to a single complex, we see that the species was named on quite tenuous grounds. In fact, one of its namers subsequently sank it into *Homo erectus*, a move which has never been seriously challenged. It is concluded that a biologically meaningful species was not represented by this group, based on only one single mandible.

Australopithecus boisei does in fact represent a good species, albeit by a very narrow margin. Valid traits represent 51.5% of the total traits listed, while 45.5 % were not. When a direct comparison is made between the two 'robust' species, we again see 50% of the traits which were proposed as being able to separate out the species are valid. It is therefore concluded that *Australopithecus robustus* and *Australopithecus boisei* are both good species, but again by a narrow margin. This narrow margin appears to lend weight to the conclusions of others that they represent a superspecies (Tobias, 1968) or a species complex (Johanson and White, 1979; White et al., 1981). This close relationship between the two requires some serious future consideration.

Paraustralopithecus aethiopicus provides a situation quite akin to that faced with *Telanthropus capensis*. It also was named based on only a single (edentulous) mandible, which again is not deemed to be sufficient evidence of a new species, let alone a new genus. However, in combination with the analysis performed upon *Australopithecus aethiopicus*, the outcome is somewhat altered. The majority of the traits used to define that species (based on a single skull) are valid, and as such indicate that this species may in fact be valid. It is therefore tentatively concluded that *Australopithecus aethiopicus* represents a valid taxon, pending more fossil discoveries.

The next species, *Australopithecus afarensis* provides again more difficulty. Exactly 45% of the traits separate the chimpanzee species, and exactly 45% do not provide separation. At the very least, this casts some serious doubts on the validity of the species, and many of the traits used to define it. Further resolution of the problem will be achieved when the traits used to specifically distinguish between *Australopithecus afarensis* and *Australopithecus africanus* are analyzed.

In the comparison between *Australopithecus afarensis* and *Australopithecus africanus*, it was noted that only 40% of the traits listed were able to differentiate between the species of chimpanzee, while 50% were not able. This would appear to indicate that the two groups should perhaps not be separated, since the majority of the traits said to show such separation in fact, cannot do so. When the list of traits is modified to remove those traits which were said to be able to separate *Australopithecus afarensis* and *Australopithecus africanus* but could not, the results are quite similar. Of the remaining traits, 36% provided separation, but 48% could not. This strengthens the argument that the two taxa are not sufficiently different to require a specific division. Again, the majority of the traits said to be able to separate out the two could not provide any separation in an outgroup comparison. It is therefore concluded that *Australopithecus afarensis* does not represent a species separate from *Australopithecus africanus*. They are more likely both members of the same evolving lineage, sampled at different times.

The latest hominid species to be named, *Australopithecus ramidus*, provides the clearest resolution in this study. Of the traits used to name this new species, only 25% can separate out the chimpanzee species, while 69% cannot. It is quite clear that this taxon was premature, and that it does not appear to be valid. Further fossil discoveries may ameliorate this conclusion, as it was originally based on only a small number of fossils. Nonetheless, it would appear that this species was prematurely named.

6.3 Conclusions - Genus level

The taxonomic status of the genera of the australopithecines can be summarized as such. The genus *Australopithecus*, with 60% of its traits separating, and only 29% not, appears to be a valid genus. The majority of its traits can distinguish between *Gorilla* and *Pan*, and as such are acceptable as defining criteria. *Australopithecus* is clearly a valid genus, separate from all other hominid genera.

Paranthropus too appears to represent a valid genus, again with the majority of its traits (61%) separating, while only a minority (29%) cannot. This adds strength to the arguments that *Paranthropus* should be re-erected to house the 'robust' material from East and South Africa. There are 26 traits which define this genus, and which are capable of distinguishing between *Gorilla* and *Pan*, while only 12 do not.

Looking at the test between 'robust' and 'gracile' taxa, we see further evidence that *Paranthropus* may in fact represent a valid genus. Thirty traits were listed out which could also separate the two genera of extant apes. *Paranthropus* separates out from *Australopithecus*, although by only a small margin (25 traits do not separate). The fact remains, however, that *Paranthropus* may in fact represent a valid genus.

Zinjanthropus is troublesome in that despite being considered an invalid genus for many years by virtually all, it does appear to separate out well. *Zinjanthropus* housed one and only one specimen in its lifetime, the OH5 skull. When the traits used to define the genus are pared down to exclude invalid traits (as did Robinson, 1960), we are left with only 11 traits to define a biologically valid genus, a difficult position to defend. It is concluded here that the genus *Zinjanthropus* was justifiably sunk by Leakey et al. (1964), as was confirmed by Tobias (1967b).

The newly named genus *Ardipithecus* does not appear to represent a valid taxon, as only 38% of its traits provide separation, contrasted to 56% which do not. The majority of the traits argue against it being a biologically valid taxon separate from all other hominid taxa. It again appears that this was a prematurely named taxon.

From the above discussion we can see that the most tenable taxonomic scheme is that of Tobias (1968). *Australopithecus africanus*, *A. robustus*, and *A. boisei* are all valid species. Also included in this list is *Australopithecus aethiopicus*. Further, it might also be more strongly claimed that the 'robust' australopithecines are in fact represented by their own genus, *Paranthropus*. These taxa are accepted as valid to the exclusion of all others. The next step is now to determine the exact relationships between these australopithecine species and our own genus, *Homo*.

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