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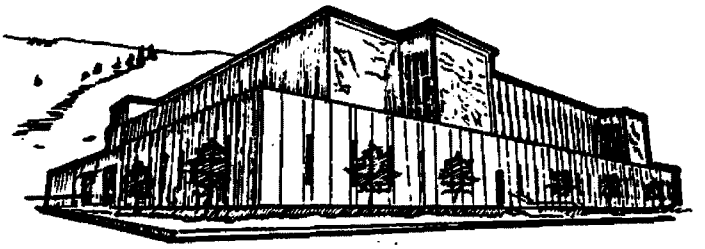
Adaptive radiation of the Plio-Pleistocene hominids : An ecological approach

Patrick Light
The University of Montana



The Adaptive Radiation of the Plio-Pleistocene Hominids: An Ecological Approach

By

Patrick Light

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The taxonomic nomenclature and phyletic relationships of the australopithecines and the other Plio-Pleistocene hominids, a morphologically diverse group of hominids, has been a source of controversy since the discovery of the first australopithecine in 1925. Numerous phylogenetic trees have been proposed, but none has given much attention to the environmental conditions and how the australopithecines may have adapted to these conditions.

A hypothetical model of human evolution is constructed, based upon a search of available literature on the fossil, environmental and archaeological evidence of human evolution; the model synthesizes the strong points of present theories with the current paleontological records.

Differences in the environments within eastern Africa and between eastern and southern Africa led to different adaptations by the various australopithecine populations. In South Africa, a population of gracile australopithecines, *A. africanus*, descendants of *A. afarensis*, appeared by 3 million years ago. Because the environment in South Africa is more homogeneous than the Rift Valley of eastern Africa, the entire population adapted in the same way, developing a specialized cranio-dental complex, to eat vegetable matter more efficiently, and somewhat larger body to stay warmer in the cold season. This robust form, *A. robustus*, was successful until the appearance of *Homo erectus*, but it was incapable of adapting rapidly enough to the new competition and became extinct. *H. erectus* survived as the only hominid, capable of adapting to life anywhere in the world.

In eastern Africa, the mosaic of micro-habitats led to competition between two populations occupying different habitats. This caused one population to evolve as a specialized vegetarian, the hyper-robust *A. boisei*, developing the same adaptations as *A. robustus*. The other population evolved bigger brains which allowed greater problem-solving ability and cultural capacity and became *H. habilis* and, eventually evolved into *H. erectus*. The hyper-robust form, restricted by its physical adaptations, became extinct.

The study of human origins is an attempt to determine a historical sequence of events from inadequate data. It is evident to all that the data are inadequate at present. It is highly probable that they will always be inadequate, because they must remain ambiguous in the sense that they will be consistent with more than one possible interpretation. . . .

Our task, then, is to take inadequate data, to reject interpretations that do not fit these data, and judge the probability of the usually still multiple possible interpretations that remain.

-G. G. Simpson (1950:55)

The fit must be good for the argument from analogy to appear plausible; but plausibility does not prove causation.

-L. R. Binford (1981:285)

Imaginative insight must stop well short of delirium.

-Calvin Wells (1965:33)

The new data show that the simplest hypothesis concerning early human evolution is incorrect and that more complex models must be devised. The single species hypothesis has served a useful purpose in focusing attention on variability among the early hominids and also on the ecological consequences of hominid adaptations. Alternative concepts, especially those concerning niche divergence and sympatry, should now be formulated.

-R. E. F. Leakey and Alan C. Walker (1976:573-574)

Entia non sunt multiplicanda praeter necessitatem.

-William of Ockham

FOREWORD

The origin of this thesis most clearly began last May when I was taking my written comprehensive examination for the Master's Degree. One of the question asked for an explanation of the variability observed in the australopithecines. I cannot say that I had a flash of inspiration then and there, and saw the complete idea. But, I did see that the usual explanations were not sufficient and that, perhaps, the north-south/tropical-temperate distribution of the australopithecines, coupled with the apparent presence of *Homo habilis* only in East Africa, might be of some importance. In answer to the question, I sketched out a rough and vague outline of my idea. I hesitated for a few moments before I did this, because I was not sure that a Master's comprehensive exam was the place to be presenting a new theory. However, I decided it was as good a place as any, and if I did not write it down while I was thinking about it, I would probably forget most or all of it.

After writing it down I pretty much did forget it, the quarter was coming to an end and I was busy with plans to go to Africa for most of the summer to attend The National Museum of Kenya and Harvard University's Koobi Fora Palaeo-

anthropological Field School. It was while I was at Koobi Fora, in the wind, dust, sun and heat, that the idea re-emerged. I had time to think about it; I find silence and space a great help in thinking. I developed the idea and decided that it had potential. It also had potential as a thesis topic. I already had one idea for a topic, but thought that I should come up with at least one more if not five or six. Besides, I was getting bored with my first topic.

Anyway, the more research I did the more workable I believed my hypothesis to be, and the more I wonder why someone else did not think of this before. Around the time I was getting my proposal approved, I was scrounging around in some notes I had written around the time I was an undergraduate (it has been a while, my B. A. stands for "before *afarensis*") and I found several phylogenies that I had constructed; except for the addition of the "black skull" (KNM-WT 17000), a few years ago, the phylogenies are basically what I present here. The diagrams, with some notes, were the first faint glimmer of the present work. Who knows how or when we really think of something?

I'm basically a "loner." I do many things alone, but I could not have done this thesis by myself. It was Isaac Newton, I believe although I could be wrong, who said that if he saw further, it was because he stood on the shoulders of those who preceded him. A very large part of this pre-

sent work is based upon the work and the ideas of others. Many, but not all of them, are listed in the References Cited.

There are others, though, who have had a hand in helping me write this thesis, and I should like to thank them for their help. Marianne Fahr and her staff at the Interlibrary Loan of the University of Montana, obtained for me many of the articles that I have cited. I also need to thank them for allowing me to use several years worth of Interlibrary Loan requests in a few months. I wish to thank Dr. Harry V. Merrick, Dr. Craig S. Feibel, Marsha Smith, John Kimengich, and the rest of the staff of the Koobi Fora Field School for their efforts in operating the field school and for providing me the opportunity to learn more about Africa and the australopithecines. Dr. Sandy Smith has been an immense help with advice, encouragement, and her editorial skills. I thank her for that, and for directing my thesis committee. Thanks also to Dr. D. C. Taylor and Dr. David Bilderback, the other members of my committee, for their help.

Of course, only I am responsible for any errors contained in this thesis, and all opinions are my own and do not necessarily reflect the opinions of the members of my committee or anyone else. Possibly, this thesis is the fault of my parents. For years they kept suggesting that I return to school; one day I listened to them and here I am.

Actually, they have been a constant source of support and encouragement, and I owe them much. Finally, I wish to apologize to my wife. I thank her for the typing she did, amazingly enough she was able to read almost all of the scribbles that I pass off as handwriting, but mostly I must apologize for having been so trying at times (much of the time). I fear that I sorely tried her patience.

P. L.

LIST OF FIGURES

CHAPTER ONE

INTRODUCTION

HISTORY OF AUSTRALOPITHECINE TAXONOMY

> It is all too easy for us today to look back- and down-on taxonomic and phylogenetic conclusions that palaeontologists reached about their finds up to the third decade of our century. But it should instead be astonishing to us that early interpretations of human evolution were even remotely right, considering the handicaps that palaeontologists worked under.
>
> -R. B. Eckhardt (1976:469)

In 1925, Raymond Dart announced an entirely new hominid taxon, *Australopithecus africanus* (Dart 1925). Dart claimed that the fossil skull, which had been found at Taung, South Africa in 1924, represented a human ancestor. This caused a great and continuing controversy. Evaluation of the merits of Dart's claim was hampered by the fact that the skull was that of a juvenile; very few people accepted it as a hominid. Most experts said it was an ape (Simons 1968), and that the hominid features were due to its being a juvenile who had not yet fully developed the specializations that marked its pongid heritage. For ten years, Dart's claim for the hominid status of the Taung skull (1925, 1926) failed to gain any general acceptance (Campbell 1988; Tobias 1985a). Only one man, Robert Broom, had come to believe that Dart

was right. Broom, who had gone to Johannesburg and examined the fossil skull, set out to find more evidence that Dart was right. It was not until the early 1930s that Broom was able to begin his search (Campbell 1988), and it was several more years before he was able to find what he had been searching for. In 1936, while he was visiting the limestone quarry at Sterkfontein, the mine owner showed him a fossil skull that had been blasted out of the limestone matrix during quarrying operations. Broom recognized it as being similar to the Taung skull, but that of an adult. Initially, he decided that it was of a different species from the Taung skull and he named it *Australopithecus transvaalensis* (Broom 1936). A year later, after (one presumes) further study and more thought, he decided that the differences were more than specific and he renamed it *Plesianthropus transvaalensis* (Broom 1937). Thus began something of a tradition in australopithecine taxonomic nomenclature. The hominid finds from each new site were each given a new taxonomic name. In some cases, Swartkrans and Olduvai, the fossil hominids found at each site were divided into two taxa. It was not until the 1960s, a quarter of century and many names later, that the reverse trend set in (Tattersall 1986).

In 1938, Broom continued his fossil finding and naming with a skull from Kromdraai which he named *Paranthropus robustus* (Broom 1938). The beginning of World War II brought a temporary end to the search. Further work began

after the end of the war. Raymond Dart, who had had little to do with anthropology after the initial finds, returned to the field with the finding of a skull fragment at Makapan. He believed that he had evidence of its association with fire, so he name it *Australopithecus prometheus* (Dart 1948a). Two years later, at Swartkrans, Broom made his last find of an australopithecine, the one he named *Paranthropus crassidens* (Broom 1949). It was also at Swartkrans, the next year, that Broom and his assistant, J. T. Robinson, found the remains of a more advanced hominid, one they believed was ancestral to modern man; they named it *Telanthropus capensis* (Broom and Robinson 1950).

The discovery of so many fossil remains of the australopithecines led to a general acceptance of them as hominids (e.g. Keith 1947). The controversy over them shifted; arguments no longer revolved around their being hominid or pongid. The debates were about their being fully bipedal or incompletely so (Clark 1955, 1966; Napier 1964), whether they were directly ancestral to *Homo sapiens* or a side branch (Leakey 1963; Osborn 1929; Wood-Jones 1947), if they used and/or made tools (Bilsborough 1971; Oakley 1970), whether they were carnivores (Ardrey 1961; McBroom 1968), and in what kind of environment they lived (Leakey 1963; Robinson 1963b). There was also much debate about the taxonomic names to be used and the dating of the sites (Howell 1955; Oakley 1954).

After 1949, there was a hiatus in the discovery of new fossil hominids. Work continued at several South African sites and more fossils were found and added to the collection of australopithecine fossil bones; but the finds were more of the same kind of fossils.

Until 1959, all known finds of Plio-Pleistocene hominids had come from South Africa. (See Figure One for a geologic timescale.) Two separate finds at Sangiran, Java of teeth and mandibular fragments, had been named *Meganthropus paleojavanicus* (von Koenigswald 1945). These were, and still are, of uncertain affinity (Pope and Cronin 1984). Some said that they were Asian australopithecines (Robinson 1953a, 1955, 1963b) and others relegated them to the taxon *H. erectus* (Pope and Cronin 1984). In 1959, working in Olduvai Gorge, Tanganyika, now Tanzania, Mary Leakey, discovered a skull. It was a significant find; the skull was datable (1.75 million years ago), and it was found on what is believed to be a living floor, and in context with stone tools (Oldowan pebble tools). L. S. B. Leakey name it *Zinjanthropus boisei* (Leakey 1960) and claimed that it, not the australopithecines, were directly ancestral to man. Others believed that it was an East African australopithecine (Day 1986). By 1964 though, he (Leakey 1966; Leakey, Tobias and Napier 1964) had become convinced that "Zinj" was an East African australopithecine and, therefore, not ancestral to man and not responsible for making the pebble

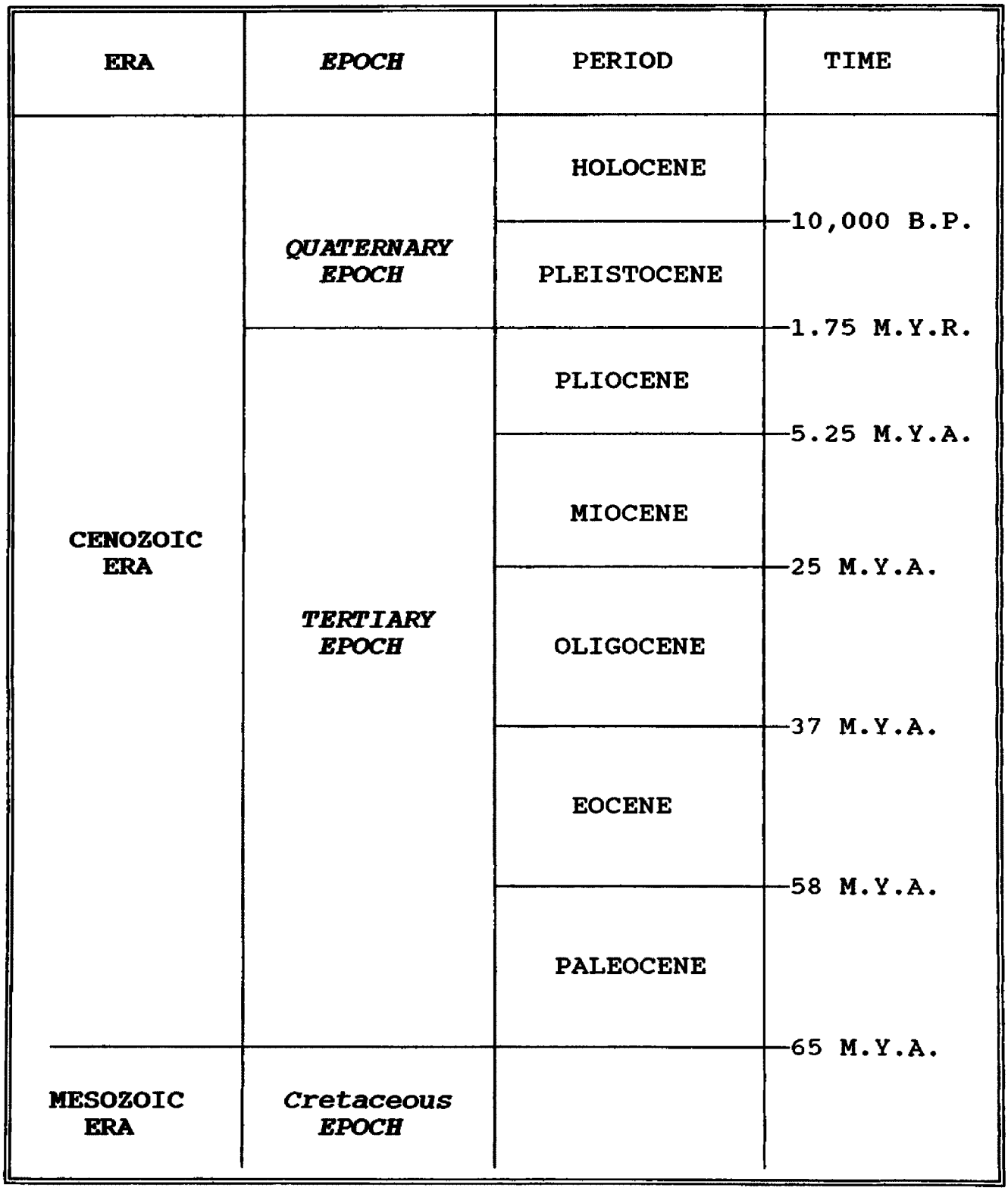

FIGURE 1. Geologic timescale of the Cenozoic Era.

tools with which it had been found. He believed that another hominid, the fragmentary remains of which he named *Homo habilis* (Leakey, Tobias and Napier 1964), had made the tools. The known range of the australopithecines expanded again in 1966 when Yves Coppens announced that he had found a hominid fossil at Koro Toro, in Chad. Although he created an entirely new taxon for it, *Tchadanthropus uxoris*, it is widely believed to be an australopithecine, very similar to *A. africanus* (Simons 1967).

Throughout the 1970s, there were many more finds of Plio-Pleistocene hominids in Africa, primarily in East Africa: at Omo, Hadar, Koobi Fora and Laetoli. Of all the finds, only one new name has gained general, if disputed, acceptance: *Australopithecus afarensis* (Hinrichsen 1978, Johanson, White and Coppens 1978). Several other attempts to name new australopithecines have generally been unsuccessful, e. g., *Australopithecus aethiopicus* (Arambourg and Coppens 1968) and *Australopithecus walkeri* (Ferguson 1989).

After so many years of little or no resistance to the creation of new taxa for nearly every new fossil hominid, a reaction set in within the scientific community. It has become difficult for a new name to gain any kind of general acceptance, many of the previous names are considered to be synonymous and, therefore, invalid (see Appendix I for a partial list of taxonomic names and their synonyms). The trend had begun earlier, after the first series finds.

At the same time that Broom (1950) was dividing the australopithecines into three supergenera with at least three genera and five species, Ernst Mayr (1950) was arguing that the australopithecines were only a species of the genus *Homo*: *H. transvaalensis*. Mayr was a harbinger of things to come. As further fossils were discovered, Mayr changed his mind (Mayr 1963) deciding that the australopithecines were sufficiently different from *Homo* to warrant being place in a separate genus. Also, there was evidence that the australopithecines, themselves, differed enough to be divided into several species.

Before Mayr changed his mind, Robinson (1954) had argued, rather persuasively, for dividing the australopithecines into two genera, with one species in each genus: *Australopithecus africanus* and *Paranthropus robustus*. He based his arguments on the concept of dietary specialization; *A. africanus* was a carnivore and *P. robustus* was a vegetarian. Robinson argued that *Paranthropus* was highly specialized dentally as a vegetarian, occupying a different niche than *A. africanus* and, therefore, should be placed in a different genus. His dietary hypothesis (Robinson 1954a, 1954b, 1961, 1963b) gained fairly wide acceptance, at least as a model. But most anthropologists believed that the difference was only specific (Walker 1976), not generic, and placed the australopithecines in one genus with two species: *A. africanus* and *A. robustus*. For quick and easy reference,

and to avoid the question of correct taxonomic nomenclature, these are often referred to as the "gracile" and "robust" australopithecines, respectively.

When Louis Leakey announced (1960) the discovery of *Zinjanthropus boisei*, most anthropologists classed it as an australopithecine; even Leakey eventually accepted this view (Leakey 1966). The question was whether this "hyper-robust" australopithecine was *A. robustus* or *A. boisei*, with, perhaps, most anthropologists preferring *A. robustus*.

In 1963, George G. Simpson expressed what was most likely the majority opinion:

> It is, however hard to see how the application of more than one generic name to the various presently known australopithecine populations can possibly be justified, whatever the specific status of the populations may be. (1963:10)

Except for the swan song of the splitters: *Tchadanthropus uxoris* (Coppens 1966), there has been no serious attempt to name a new genus of australopithecines. There have been recurrent suggestions that *Australopithecus* should be subsumed in *Homo* (for example Olson 1981, 1985), but this notion has received little support.

Rather than arguing against the splitter's attempts to divide the australopithecines into a multitude of genera and species, anthropologists have spent much time arguing against the contrary position: that the australopithecines are a highly variable and/or sexually dimorphic species. The major proponents of the Single Species Hypothesis (for

instance: Brace 1971, 1972; Wolpoff 1968, 1970, 1971, 1973a, 1973b, 1976a) have since come to accept the general view (Brace 1980) that there are several species. In the 1960s and early 1970s, the common view was that there were two species (*A. africanus* and *A. robustus*) with, maybe, a third species (*A. boisei*). With the naming of *A. afarensis* (Hinrichsen 1978; Johanson, White and Coppens 1978) there was more support for three or four species: *A. africanus*, *A. robustus*, *A. afarensis*, and *A. boisei*. After the discovery of the "black skull" , KNM-WT 17000 (Walter, Leakey, Harris and Brown 1986), more anthropologists have came to accept specific status for *A. boisei*, and a four-species model. Although there have been attempts to accord specific status to KNM-WT 17000 as a fifth species, either as *A. aethiopicus* or, for procedural reasons, *A. walkeri* (Ferguson 1989), these attempts have met with little acceptance.

From the time of its naming (Leakey, Tobias and Napier 1964) *Homo habilis* has been a controversial taxon (Robinson 1965; Simons, Pilbeam and Ettel 1969). Some of the criticisms had been that it was simply an advanced gracile australopithecine (Bruce, Mahler and Rosen 1972) and should be considered as either *A. africanus* or *A. habilis* (Campbell 1988). There was some suggestion that Leakey, Tobias and Napier were right about its generic status as *Homo*, but that it was not specifically different from *A. africanus*. *A. africanus* was more properly *H. africanus* (Olson 1978, 1981).

Part of the controversy over the validity of the taxon *Homo habilis* was due to a claim that a skull (KNM-ER 1470) was attributable to the genus *Homo*, and that it was dated, at least, 2.61 ± 0.26 M. Y. A. (million years ago) (Fitch and Miller 1976; Leakey, Mungai and Walker 1971), or even as old as 2.9 M. Y. A. (Leakey 1973). It is a very advanced hominid for such an old date. Once the revised date of 1.88 M.Y.A. (± 0.02 M. Y. A.) (Day 1986) gained general acceptance, so did the taxon *H. habilis*. Now it is fairly well accepted (Campbell 1988; Day 1986) that whatever the "habilines" are to be called taxonomically, they represent a connecting link between the australopithecines and *Homo erectus*, the first undoubted member of the genus *Homo*.

Part of the confusion in taxonomic nomenclature systematics is due to a change in ideas of how much variation is acceptable within a species. The older typological concept has been replaced, but not totally, with the concept of species as a population. R. B. Eckhardt, clearly and succinctly, described the differences:

> In systematics one of the most evident developments has been the replacement of a typological species concept (one in which species are defined on the basis of their morphological differences, usually slight) by a non-dimensional species concept (according to which two populations are accepted as separate species when they remain distinct even though sympatric and synchronic)... In palaeontology the two concepts--which can be referred to respectively as typological and populational, according to the basic units of study--lead to very different expectations of the extent and significance of intraspecific variation. In a typological framework, very slight variations from

> specimen to specimen are treated as aberrations from the ideal form of the species; any departure from this ideal is thought to signal the presence of a new type. The morphological evidence is considered sufficient in itself to decide the issue. In a populational framework, species are also delimited on morphological grounds. But as a rule wider ranges of variation are usually tolerated within the boundaries of a single species, as in neontological studies, whenever they can reasonably be shown to represent differences due to sex, age, regional ecological differences (genetic or developmental), injury and so on. While species are still inferred chiefly from morphological data, these may be supplemented by information derived from geology, palaeoclimatology, palaeoecology, archaeology and any other sources that can help to reconstruct the way of life that shaped the characteristics of the population (1976:468).

A look at australopithecine taxonomic history will show that the typological concept was dominant until the 1940s and early 1950s, but then began to change. Now, there even seems to be a reluctance to attribute any fossil remains to a new species (Leakey, Mungai, and Walker 1971). This has been a useful practice. All too often it has seemed necessary to identify the fossil species to which a fragmentary fossil bone belongs. Now there is a growing trend to wait until there are enough fossil bones to determine the amount of variation present within the population which the fossil fragments represent. These fossils are referred to in the literature by their museum accession numbers. Increasingly, even fossils that have been taxonomically classified are referred to by their accession number (KNM-WT 15000) or a name (i. e. Lucy), rather than the taxonomic name. In part,

this is due to the increase in number of fossil remains attributed to each taxon. Fossil finds no longer correspond on a one-to-one basis with a scientific name. For a long time the name *Australopithecus africanus* referred only to the Taung skull. Now it includes the fossils from Sterkfontein and Makapansgat.

G. G. Simpson (1963) identified several categories of names as they are used scientifically. Only three of these types of names need concern us here, the ones Simpson called N_1, N_2 and N_3. Simpson's N_1 name is the specimen name, it refers to a specific fossil or organism. An N_1 name could be a museum accession number (i. e. ER-1470 or MLD 1; see Appendix II for a list of some of the museum accession letter codes), or some other name (i. e. Lucy or Olduvai George). N_2 names refer to groups of individuals that are believed to form a genetically related population (deme). Campbell (1966) defined a deme as: "The unit of evolution, the breeding population (the Mendelian population, or *deme*), includes all the individuals able to mate with each other." Examples of N_2 names are Neanderthals, gracile australopithecines, and hyper-robust australopithecines. Both N_1 and N_2 names are distinct from N_3 names. An N_3 name refers to taxa and are Linnaean binomial in form (i. e. *Australopithecus boisei* or *Homo erectus*). Some of the confusion in hominid taxonomy is caused by the improper use of names, generally when an N_3 name is used for an N_1 name (i.e. using

Tchadanthropus uxoris instead of a name such as: Chad Hominid). Confusion also occurs when obsolete names are retained and used as if they were valid names.

I do not intend in this chapter to expound on the subject of taxonomy or taxonomic nomenclature. Rather, it is my intention to explain and/or define concepts and terms that I shall use throughout the remainder of this thesis, so that the reader may know what I mean when I use the various concepts and terms. Much of this discussion will be based on G. G. Simpson's work (1961 and 1963).

Webster's II New Riverside University Dictionary (1984) defines taxonomy as: "The theory, principles, and process of classifying organisms in categories." So, the place to begin might be: for what purposes are a taxonomic nomenclature used. It is probably no coincidence that Linnaeus developed his taxonomic system at a time when European exploration of the world had passed from being primarily geographic exploration (finding new lands), to explorations including a large scientific component to study the new lands. So, many organisms, new to European science, had been and were being discovered that the European folk taxonomies could not handle the flood of new animals and plants. None of these new animals and plants had accepted common names and many had no comparable European homolog. It is true that they did have names. The European explorers often got the names, often several from different groups of the

"locals." The names were usually strange-sounding, if not difficult to pronounce.

One of Linnaeus' goals was to establish a system of names that could be used by all scientists, regardless of the language they used or the name by which they knew the organism. Elk are a good example. When the Europeans explored eastern Canada and northeastern United States they encountered a large animal that a group of native Americans called "moose". This name became the one that was, and is, used commonly by everyone, including those of European ancestry. Some time later a large, deer-like animal was discovered and called an "elk," after the large European deer-like animal of that name (it was called "wapiti" by the Shawnee). A smaller deer in North America was occasionally called a "red deer" because it was thought to be similar to the red deer of Europe. The name did not stick, and, today, it is most commonly called a "whitetail." The names of deer did, and still do, cause some confusion among Europeans and North Americans.

In Europe, the members of the deer family are: elk, red deer, fallow deer and reindeer. In North America, the members of the deer family are: moose, elk, whitetail deer, mule deer (and/or blacktail deer) and caribou. Primarily, the confusion over names is with the moose, elk and red deer. When scientists studied these three animals, they decided that they were only two different types (or "spe-

cies") of animals. In the Linnaean taxonomic system the European elk was named *Alces alces* and the red deer *Cervus elaphas*. The North American elk was named, originally *Cervus canadensis*, but now is *Cervus elaphas*, and the moose is *Alces alces*. The moose is the same species as the European elk, and the American elk is the same species as the red deer.

Plant names can be even more complex and confusing. Common names can be very local in usage, a plant with a broad range can have two, three or even five or six "common" names. And like the name "elk", a common name can refer to one plant in one area and to another in a second area. Then, for various reasons, there are plants and animals that have no common name.

Linnaeus developed his taxonomic system to provide a single name that scientists could use so that everyone would know which organism was meant (i. e. the elk, *Alces alces*, or the elk, *Cervus elaphas*) and to arrange all living organisms into a categorical scheme that expressed degrees of morphological similarities and differences. Although the taxonomy was not meant to express evolutionary relationships, it has been adapted to that purpose, and extended to include fossil organisms.

Eventually a problem arose over competing scientific names. For a variety of reasons, of which hominid taxonomy provides many, an organism or fossil might have more than

one scientific name, and it became necessary for scientists to choose one of them. The International Commission of Zoological Nomenclature (ICZN) has been established to oversee and mediate all matters concerning zoologic nomenclature. Stability of nomenclature is one of the basic goals of the ICZN. The ICZN has decided that priority of publication would be the primary criterion for determining the correct scientific name.

The Linnaean taxonomic system identifies, not individuals, but groups of organisms called "species". Although everyone seems to know what a species is, the concept has defied easy definition. Most definitions use as a base the interbreeding capabilities of a population of organisms (a "deme") living in their natural state. This works fairly well for animals that are only capable of sexual reproduction. The whole concept of species gets quite fuzzy when one begins to deal with organisms that reproduce, either solely or alternatively, by other means. But, at least with living organisms, it is possible to study and/or test the reproductive boundaries of a breeding population and establish some sort of limit to that species. With fossil organisms, this is not possible. The paleontologist and paleoanthropologist, and anyone else who studies fossils, must use other means of defining species. He must also deal with time, and with an entity called a "palaeospecies," which is different from other kinds of species. Simpson

(1961:155) defined a palaeospecies as "temporally successive species in a single lineage." He then contrasted palaeospecies with other forms of species:

> They [palaeospecies] are a distinctly different kind of a thing from a genetical or other contemporaneous species,... . They can both be viewed as aspects or states of the evolutionary species: one [palaeospecies] is a segment of an evolutionary species delimited in a certain span of time; the other [contemporaneous] is a cross section of an evolutionary species at any one time (1961:166).

It is neither possible, nor correct, to apply the same criteria in defining a palaeospecies as one uses for a species.

CHAPTER TWO

HYPOTHESIS AND METHODOLOGY

> A far more extensive ecological analysis of man's early environment, both in terms of its enemies and its advantages is needed before we can gain a clear picture of the life of that old-fashioned mammal who descended upon the grass,...
> -Loren Eiseley (1952: 4)

In 1866, Ernst Haeckel (1834-1919) coined the word "oecology" as the science of the economy of nature (Stauffer 1957:138, 140), referring to the relationships between organisms and the organic and inorganic environment. The introduction of the term oecology did not mark the introduction of a totally new concept. Haeckel, like Darwin from whom he got some of his ideas, brought together ideas and concepts that were already about and gave them form and substance and, in this case, a name (Stauffer 1957).

Now, almost 125 years later, although we have changed the spelling, we have not really changed the sense of the word. Ecology is still "...the study of the interrelationships of organisms to their environment,..." (Wallace 1979: 2) or "...the study of the structure and function of nature," (Odum 1963:3). Ecology's emphasis is not on the individual but on populations, communities, ecosystems, and the biosphere (Odum 1963). As one more definition (Half-

penny, Ozanne and Biesiot 1989:3) explains:

> Ecology, by definition, includes the study of the functional relationship between the environment and the organism. The study of either the environment or the organism by itself is not ecology. Only when the link is made between the two does the study become ecology.

When it comes to man and ecology, the public tends to become confused and to think that ecology is either recycling, saving the whales and not depleting the ozone layer, or it is about Eskimos hunting seals, the !Kung gathering mongongo nuts, or the Yanomamö with their slash-and-burn horticulture. For many cultural anthropologists, human ecology may be about the Eskimos, !Kung, Yanomamö, and everyone else. But paleoanthropology is different, the organisms are extinct and the environment has changed; even the landscape has been altered, often radically. The paleoanthropologist's primary goal is to reconstruct the course of human evolution, man's phylogeny.

As Johanson and White wrote:

> The ultimate goal of human evolutionary studies is to understand phylogenetic and adaptive patterns among the hominids. Such understanding has sometimes been hampered by an emphasis on naming the hominid specimens. We recognize the usefulness of classifying fossil materials, and we agree with Simpson that 'classification is not intended to be an adequate expression of phylogeny, but only to be consistent with conclusions as to evolutionary affinities'. [G. G. Simpson. 1963. in Classification and Human Evolution, S. L. Washburn (ed.). Aldine, Chicago. p. 1] (1979:328).

As noted above the Linnaean taxonomic system was not originally meant to be an evolutionary taxonomy; it has

been altered to express evolutionary schemes of paleontology. To construct an evolutionary taxonomy requires that the general course of a group's evolution be known (Groves and Mazák 1975:226). One cannot use taxonomy to construct phylogeny because, in an evolutionary scheme, taxonomy reflects phylogeny. Ecology, paleoecology in this instance, should serve to help reconstruct a phylogeny. Ecological theory can be used to help explain why an organism, or better, a population was changing as adapted to that environment. By knowing the niche that a population filled and how the organisms adapted to that niche, it is possible to rule out some phylogenetic models because they are not reasonable. For instance, the ancestor of all land animals is most likely to have lived in swamps, seasonal rivers or tidal zones and not to have lived in the ocean deeps.

For the Plio-Pleistocene hominids (by which I intend to refer to the early hominids that preceded *Homo erectus* (Sigmon 1977)), there has been no dearth of phylogenies created to explain the relationships, or the lack of relationships, between the various known fossils (for example: Andrews and Martin 1987; Brace, Nelson and Korn 1971; Brain 1987; Broom 1938, 1950; Broom and Robinson 1950; Campbell 1973, 1988; Chamberlain and Wood 1987; Clarke 1985a; Dart 1925, 1955; Grine 1985; Groves and Mazák 1975; Howell 1978; Johanson and White 1979; Johanson, White and Coppens 1978; Leakey 1966; Clark 1964; Mayr

1950; Olson 1981, 1985; Pfeiffer 1969; Pilbeam 1972a; Poirier 1973; Robinson 1953a, 1953b, 1954a, 1955, 1963a, 1965, 1972; Tattersall, Delson and Van Couvering 1986; Tobias 1980; Walker, Leakey, Harris and Brown 1986; Wolpoff 1968, 1973b; Wood 1985; Wood and Chamberlain 1987). None of the phylogenies known to me really considered the ecology of the hominids involved, as a basis for constructing a phylogeny. All the phylogenies are based upon morphologic similarities or dissimilarities. Other than Robinson's "dietary hypothesis" (1954a, 1963b), by which he only tried to explain the presence of two species by postulating different morphologies based on two different diets, probably caused by two different environments. The concept of ecology has been ignored in all the phylogenies. Anthropologists do not ask why different niches led to different adaptive patterns, or rather, the reverse, how did the different environments of the australopithecines lead to different adaptive strategies in various australopithecine demes.

As a group, the australopithecines are morphologically diverse; this has been part of the cause of the vast number of taxonomic names being given to the fossil specimens. This morphologic diversity, whether it be generic, specific, or subspecific, is characteristic of organisms that have entered a new econiche. The organisms expand in the new niche, in a sense, "exploring" the limits of its new adapta-

tion. As G. G. Simpson wrote: "Progression, splitting, and accompanying divergence clearly tend to lead to increasing diversification or expansion, in evolutionary terms frequently an adaptive radiation, . . . (1961:203)."

The first australopithecines succeeded in invading a new econiche, one that had not existed before. At first there was little or no competition within that niche, and they increased in number and in geographic area, until they reached the limits of the niche. Then they met competition: themselves. Each population differed slightly from the others. They occupied the same basic niche, but each population's particular niche was slightly different. Some populations occupied a gallery forest, some a tropical savannah, and others a temperate savannah. Each population adapting to slightly different conditions, dividing the niche into smaller niches. Each population was adapting to a more precise niche, and gaining a competitive edge over other, similar, but not identical, populations. This allowed more populations to exist, or would have. One population seems to have evolved a way of life that allowed it to replace all the other hominid populations and expand far beyond the limits of these other populations.

Other than the dryopithecines, I can think of no other group of primate fossils that has been taxonomically classified in such a wide assortment of genera and species as have the australopithecines; nor can I think of any other

group that has engendered quite as long a debate about its "correct and proper" classification. The australopithecines are a morphologically diverse group; it is my hypothesis that the morphologic differences observed in the australopithecine fossils represent the effects of adaptation to a wide range of habitats. Also, it is my hypothesis that competition between several of the australopithecine populations led to the evolution of *Homo*.

Taxonomies are based, and rightly so, on morphology. However, to base a phylogeny solely on morphology is to ignore other data that can be useful helping to "sort out" confusing morphologic patterns (Delson 1977). I shall not discuss morphology as much as I will be discussing environmental factors and how an organism (or population of organisms) might adapt to them. I do not plan to offer new facts, rather I intend to use the facts as now known and to create a synthetic model from them. I will use the data gathered by a large number of people, examine it in an ecological frame of reference, and construct a plausible model of how the Plio-Pleistocene hominids (as shown by their morphology) may have adapted to the various environments of the African Plio-Pleistocene. To a certain extent, the ecological approach involves only two things: the organism under study, and its environment. But, the ecological approach is far more than that, it is an holistic approach. The environment is more than the surrounding

plants and weather. It includes those, and the other animals, rocks, soil, wind, sun, water, and time, all those "things" that affect us, whether we know it or not. It is this holistic approach that I intend to take, synthesizing strong points of present theories with the current paleontological record, constructing an hypothetical model of human evolution that better explains the evidence as currently known. I am not the first to take a broader approach, others have done so before (Robinson's Dietary Hypothesis is an example), just not to the extent that I intend to use it.

CHAPTER THREE

THEORIES OF AUSTRALOPITHECINE VARIATION

> The whole process of natural selection is basically an ecological process- the problems of adaptation in structure and behavior are ecological problems.
>
> - Marston Bates (1960:566)

The proliferation of australopithecine fossils eventually led to speculation. To many anthropologists, the South African fossils appeared to fall into one of two groups: either "gracile" or "robust". One of the first explanations put forward to explain this difference, was that the gracile australopithecines were females and the robust australopithecines were males. The gorilla (*Pan gorilla*) was offered as a modern example of such sexual dimorphism.

However, as more fossils were found, it appeared that the gracile/females were always in deposits thousands of years older than those deposits in which the robust/males were found (Brock, McFadden, and Partridge 1977; Howell 1955; Maguire 1985; Maier 1977; Partridge 1985a; Turner 1986; Vogel 1985; Vrba 1974, 1985b). Although this hypothesis had much to offer as to why the australopithecines

were now extinct, it was quite unsatisfactory on other counts.

In 1961, J. T. Robinson offered an hypothesis to explain the two differing morphologies (Robinson 1961, 1963b). Robinson's hypothesis (generally known as the "dietary hypothesis") postulated two different and successive populations of hominids, adapted to two different niches in two different climates.

One population, the robust australopithecines, were vegetarians who lived in a generally humid environment (Robinson 1961). They had adapted to their vegetable diet with enlarged molars, reduced canines and enlarged chewing muscles. The other population, the gracile australopithecines, were tool-using hunters and lived on the flesh of their prey. The lightly built, and presumably swift and agile, gracile australopithecines lived in a dry climate, hunting the many herbivores who eked out a living in the arid savannah. These gracile australopithecines were thought to be the immediate ancestors of the genus *Homo*.

Robinson (1954a, 1954b, 1961, 1963b) also argued that these two populations represented two differing adaptive trends and, therefore, belonged to two different genera: *Paranthropus* and *Australopithecus*. Robinson's argument that two related species, with a somewhat similar morphology but, different ecological roles, belonged in different genera (Robinson 1961, 1963b) is a point I shall return to later.

The basic postulate of the "dietary hypothesis" was that the two different strategies for obtaining food from the environment, carnivore and vegetarian, would lead to two different adaptive morphologies. Most of the morphologic differences would be related to the difference in diet and would occur in the teeth, jaws and cranium. The differences were there: it seemed obvious that the robust fossils had been adapted to masticating large quantities of vegetable matter (Robinson 1954b, 1961, 1963b). It was not so obvious that the gracile australopithecines had dental adaptations for a carnivorous diet. And, as for their tool-use, there was no evidence linking them directly with stone tools (Robinson 1961). Raymond Dart's "osteodontokeratic" culture (Dart 1948a, 1948b, 1949, 1953, 1956, 1959a, 1962a, 1964, 1971; Hughes 1954; Sutcliffe 1970) was highly controversial and, eventually, all his evidence for it was discredited (Bilsborough 1971; Brain 1981; Hill 1976; Shipman and Phillips 1976; Shipman and Phillips-Conroy 1977).

Also discredited was the theory of African pluvial (Deacon 1983; Flint 1959). This theory suggested that the Pleistocene climate in Africa had cycled through a series of "pluvials" (rainy periods) and "interpluvials" (arid periods) similar to the glacial/interglacial sequence of Pleistocene Europe.

As the pluvial theory lost credence and it appeared that South Africa had never, at least as far as the Plio-

Pleistocene is concerned, been much rainier than it is now (Deacon 1983; Flint 1959), it became difficult to argue for a shift from vegetarianism to carnivorism because the climate became increasingly arid (Robinson 1961). Further difficulties arose from the accumulating evidence that the gracile forms were geologically older than the robust forms (Howell 1955; Vrba 1985a). Further, there was evidence that the robust australopithecines had coexisted with *Homo erectus* (Brain 1985; Broom and Robinson 1950; Olson 1978; Tobias 1973, 1985b) and could not, therefore, be ancestral to man in any way. The evidence appeared to support the idea that the populations of gracile australopithecines, whatever their diet, had diverged throughout the course of time. One population had become strict vegetarians and the other had become the big-game hunter *Homo erectus*. This scenario was not without its critics.

Robinson had a good idea, the concept was valid, it was not supported by the facts (or what we believe to be facts). Basically, life, reproduction and natural selection are all about eating, subsistence (thereby surviving for another day). Every organism gathers energy from its environment, uses some for daily survival and the extra for reproduction. If one does not eat, one does not reproduce. It is not quite as simple as that of course, but feeding strategy is a major part of a species' adaptation. Robinson was correct to emphasize this (Robinson 1961 and 1963b), and also to ask

why these populations took different adaptive courses. We are now in a much better position to ask these questions again. We need to ask what adaptive strategies might the Plio-Pleistocene hominids have taken, what would we find in the fossil record and how well does the fossil record support these postulated answers?

Actually, there have been two versions of what is called the Single Species Hypothesis. The first, which I discussed above, was the hypothesis that the gracile australopithecines were the females of the species and the robust australopithecines were the males. This hypothesis foundered on the fact that the two morphologic types were neither synchronic nor sympatric.

The second single species hypothesis (Brace 1972; Brace, Mahler, and Rosen 1972; Brace, Nelson, and Korn 1971; Wolpoff 1968, 1971, 1973a, 1973b, 1974, 1976a, and 1976b) is a more sophisticated and complex argument. The hypothesis has two parts: the first based on dental evidence and, second, on the Competitive Exclusion Principle.

The original concept of a single australopithecine species was based on the observed differences in the osteological evidence. The fossil bones (primarily cranial) fell into two populations. Robinson (1954a; also Clarke 1985a) argued that the differences were generic, others (Clark 1964), that they were specific, and some said that they were sexual (Brace 1972; Brace, Nelson, and Korn 1971; Wolpoff

1973b, 1976b). The theory that the differences were sexual foundered on an inability to demonstrate coexistence of the two supposed sexes. The second single species hypothesis is based, not on sexual dimorphism, but on the variation in length-breadth ratio of the teeth, primarily the molars. In particular, Wolpoff (1971, 1973a, 1973b, 1974, 1976a, 1976b) has argued that the teeth represent a single, although highly variable (polytypic), species. Based on a statistical analysis of the teeth, Wolpoff argued (1971, 1973a) that the teeth could not be divided into two populations. Although the teeth do form two groups (roughly identical to the two groups the osteological evidence forms), Wolpoff argued (1973b) that they are not distinct. They overlap in range and, therefore, represent only one species. For Wolpoff (1971), separate species require non-overlapping distribution of traits.

He did not claim that the small teeth are from females and the larger from males. To do so would place him in the same position as the holders of the first idea, explaining how a species can exist when the sexes do not coexist. Wolpoff argued (1976a) that the size of the post-canine teeth, by sex, is highly variable, some males had teeth as small as those of the females, although most had large teeth. It was the same for females. Most had small teeth, but some had teeth whose size was nearly as large as those of the largest males. This explains the bimodal distribu-

tion that Wolpoff obtained (1976a). As an explanation of the data, Wolpoff's theory is good. Since many of the teeth are not directly associated with a skull or postcranial material, it is impossible to determine the sex of the individual from whom the teeth came, or the numbers of individuals represented. If Wolpoff is correct, his model (1976b) predicts that, regardless of the overall sex ratio, the smaller teeth will be mostly female and the larger teeth mostly male. If the teeth do represent two species, about 50% of the small teeth would be from males and the rest would be from females, the ratio would be much the same for the larger teeth. But, it is not possible to adequately test the hypothesis this way.

Most of Wolpoff's evidence is a statistical analysis of the relative size of the canine and post-canine teeth. Although it is not possible to relate the anterior and posterior teeth in all instances, where it can be done, the large molars are associated with larger incisors and canines (both absolutely and relatively). It would seem reasonable, that if these teeth are all representatives of the same species, the posterior teeth and anterior teeth should be the same or similar in relative size, no matter what the absolute size. The fact (Robinson 1954b, 1961, 1963b) that the anterior teeth vary in size in the opposite direction from the posterior teeth suggests that situation. On the basis of this point, Robinson (1961, 1963b) suggested generic separation.

As for the two populations being a single species because there is an overlap in the statistical distribution of a trait, note that grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) overlap in size. They overlap in body size in the same way that Wolpoff (1976a) suggested the australopithecine populations' teeth did. Male black bears can be as large as or, larger than, female grizzly bears, but no one has suggested that they are the same species because of this fact.

The second part of the argument is that the australopithecines must be only one species because the Competitive Exclusion Principle (or Gause's Law) (Cole 1960; Hardin 1960) does not allow two species to coexist. The Competitive Exclusion Principle is not as simple as I have just implied. In clearer terms, the Competitive Exclusion Principle states that two similar species cannot coexist, indefinitely, in the same econiche. It is generally assumed that this requires the extinction of the "less fit" species. In actuality, one species need only adapt to a different econiche (<u>how</u> different is one of problems of the Competitive Exclusion Principle).

Although the validity of the Competitive Exclusion Principle (Cole 1960, Hardin 1960, Winterhalder 1980 and 1981, Wolfe 1971) is disputed, it is useful, more as an explanation of the diversity of life and the way species radiate. In the instance that two species should, by some

chance, come to occupy the same econiche, at the same place, at the same time, there would be four possible outcomes: 1) both species may become extinct; 2) one becomes extinct; 3) one adapts to a different econiche, splitting the one, formerly shared, econiche into finer subdivisions. The fourth outcome (both species change) is, to me, the most probable, although there could be variations (for instance: both species could change before one becomes extinct).

As an example of what the result might be of two species "sharing" the same econiche, the savannah of East Africa provides an example (Bell 1971). The zebra (*Equus burchelli*) and the wildebeest (*Connochaetes taurinus*) are often seen grazing in mixed herds, along with small groups of Thomson's gazelle (*Gazella thomsoni*). The zebra, in small clusters, are scattered about in among the larger numbers of wildebeest, both grazing on the grasses of the savannah. To a casual glance, it would appear that both species are competing for the same grasses. Closer scrutiny reveals that many kinds of grasses grow on the savannah, and that they are in many different stages of growth. It also reveals that the zebra are eating the upper parts of the grasses and herbs, and the wildebeest are eating the middle parts. The Thomson's gazelle eat the lower portions of the grasses and herbs. The animals are not actually in direct competition with each other, not now at least.

As a further example (Dunbar and Dunbar 1974), and one

closer, genetically, to us, there are the two species of baboons and one species of monkey in Ethiopia. The gelada (*Theropithecus gelada*), anubis baboons (*Papio anubis*), and a vervet monkey (*Cercopithecus aethiops*) share the same geographic area. However, each has "found" a separate econiche within the area to which it has adapted. These three species coexist, maintaining separate niches; they live in the same area, but exploit different micro-habitats within the area. In East Africa, three species of baboons are commonly found: the yellow baboon (*Papio cynocephalus*), the hamadryas (*P. hamadryas*), and the gelada *T. gelada*). These three baboon species normally live in the different habitats, have different forms of social organization (Altmann 1974; DeVore and Washburn 1963). Presumably, they are all descended from a single original species that diverged, different populations exploiting different types of habitat enabling more baboons to more efficiently exploit more of the environment. This is an example of adaptive radiation. (Mackinnon 1977, also gives an example of how the orangutan, *Pongo pygmaeus*, the siamang, *Symphalangus syndactylus*, and eight species of gibbons, *Hylobates* sp., use different feeding patterns and body size to create enough ecological separation to coexist.)

Returning to the East African savannah, the herbivores which exploit the grasses, just the above-ground stems and blades of grass that grow on the savannah, include: the

African elephant (*Loxodonta africana*), the black rhino (*Diceros bicornis*), the white rhino (*Ceratotherium simum*), the hippopotamus (*Hippopotamus amphibius*), the Cape buffalo (*Syncerus caffer*), the eland (*Taurotragus oryx*), the common zebra (*Equus burchelli*), the wildebeest (*Connochaetes taurinus*), the impala (*Aepyceros melampus*), Grant's Gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*), the topi (*Damaliscus korrigum*), the kongoni (*Alcelaphus buselaphus*), Kirk's Dik-dik (*Rhynchotragus kirki*), and the warthog (*Phacochoerus aethiopicus*). The Competitive Exclusion Principle, rather than limiting the number of species that coexists, is the driving force behind the diversity that exists. As Winterhalder stated:

> Although a conservative (exclusionary) interpretation of the CEP [Competitive Exclusion Principle] has the appearance of parsimony, it rests on a complicated set of highly restrictive assumptions that belie its cogency and simplicity. And, although its most apparent interpretation seems to restrict diversity, the principle actually underwrites much of the biological theory used to explain diversity (1981:102).

It is true that only one species can exist in one niche but, if that niche can be divided into finer, and finer subdivisions (more niches), more species can coexist. These would not necessarily be species, they could be subspecies, or just different populations of the same species. For that was what the descendent species of one species originally were: populations of one species.

Without becoming too deeply enmeshed in the problem/

question of speciation, I wish to review some of it. All species are composed of one or more populations of organisms. The populations are composed of individuals who are more likely to breed with one another than with an individual of another population. They share more genetic material with each other than with members of other populations; they form a "deme". There is gene flow between demes, but not as much as there is between members of the same deme. When gene flow between demes is nonexistent or nearly so, a species boundary occurs. In any species with a large number of individuals spread over a large geographic area ("large" being relative to the organism considered), there will be a number of demes. The individuals of one deme may not be much different, if at all, from individuals of another deme, but they may well be, and sufficiently so, to be called subspecies.

If a species covers a large enough geographic area, the econiche it occupies will not be absolutely identical throughout the species range.

As an example, let us examine part of the prehistoric range of the American bison (*Bison bison*), the Great Plains of the American West. Ignoring micro-habitats within the plains, such as the riverine forests, cedar breaks and coniferous-clad hills, the Great Plains was a vast expanse of flat to rolling grass-covered plains stretching from Texas and Oklahoma in the south, to Alberta and Saskatchewan

in the north, from the Rocky Mountains in the west, almost to the Mississippi in the east. But this sea of grass was not quite the same throughout its extent.

In the north, the average temperatures were much lower, and the temperature extremes potentially much lower than they were in the south. The growing season was shorter and the snow deeper and longer lasting. Rainfall varied from west to east, with more rain falling on the eastern edge of the plains than on the west, and the seasonal variation on daylight was greater in the north than in the south. All these differences meant that the Great Plains was not quite the same from place to place. As far as the bison was concerned, these variations-on-a-theme seem to be relatively inconsequential and, being a rather mobile and long-lived animal, gene flow was relatively unimpeded throughout the Great Plains. Any differences were minor and clinal in nature. A cline is the geographic variation in the expression of a trait, or trait complex, it is intraspecific and not necessarily related to subspecific designations.

To other species, these same variations may have been far more important, if they were more specialized in their adaptations rather than generalized, like the bison. I shall return shortly to the concept of specialized versus generalized.

When a species is distributed over a geographic area that contains a number of micro-environments, or a wide

geographic area that has a variable environment, there is a good probability that, given sufficient time, the various demes will adapt more specifically to the various ecological variations in the niche.

Even though the demes are not genetically isolated, the slight restriction of gene flow between the demes would be sufficient to allow a deme to accumulate enough genetic differences to become better adapted to a particular eco-niche or micro-environment. If these changes, or some other factor, contributed to an increase in the restriction of gene flow with other demes, the process could continue until genetic isolation occurred. At this point there would be, technically, a new species, even if interbreeding can or does occasionally occur.

The wolf (*Canis lupus*) and the coyote (*Canis latrans*) are two species that are adapted to two different econiches. Historically, their ranges overlapped, and they still do today. The wolf and coyote will interbreed, just as both will interbreed with the domestic dog (*Canis familiaris*). But both the wolf and coyote remain distinct species. Complete genetic isolation of a population is not the only criterion for being a species, or even a necessary criterion. As Hall stated:

> Following the wolf-coyote model the existence of two specific forms does not indicate that no inter-breeding occurred but rather that if it did occur it was not a sufficient to shatter the ecological and morphologic stability of the two groups (1977:527).

She continued, in reference to the gracile and robust australopithecines:

> It is not necessary or even wise to accept the hypothesis that ecological separation of the two hominids involved fundamental differences in choice of food with the robust form being vegetarian and the gracile form eating meat. It is more probable that the size and species of prey, and kind of hunting strategy used, differed between them (Hall 1977:527).

A population of organisms can improve its competitive edge by adapting to a narrower portion of its niche, by becoming specialized. This will make it more difficult for another, less well adapted, population to compete with the specialized population in that niche. The Competitive Exclusion Principle predicts that a generalized species, that is, a species adapted to a wide niche, will over time, evolve into a number of species that become adapted to narrower portions of that original niche. The demes will become specialized.

The diversity of life will increase, the interrelationships between the various species will become more complex and more resilient to disturbance. The existence of an individual species becomes more precarious as it becomes more specialized. A specialized species is dependent upon the existence of its particular habitat; a species that is not specialized is not so dependent upon any one habitat.

Man is a paradox. Somewhere in his evolutionary history he specialized in adapting by cultural means. He

became so specialized in cultural adaptation that he cannot exist without it. He became so specialized in a revolutionary adaptation that, like the crossopterygian fish that adapted to life on land, he entered a totally unoccupied niche--an empty niche that he occupied unhindered by competition. Man occupied most of the world's landmass with the same adaptation--the culture of the hunter/gatherer. Once man occupied the entire niche himself, then specialized versions of the hunting/gathering culture began to appear. However, since man adapts primarily by means of cultural adaptations, rather than genetically, to different niches, he remains one morphologic species. In a sense, the different ethnic groups are the species of man.

Where the proponents of the single-species hypothesis (Brace 1972; Brace, Mahler, and Rosen 1972; Brace, Nelson, and Korn 1971; Wolpoff 1968, 1970, 1971, 1973a, 1973b, 1976a, 1976b) differ from those who believe in multiple australopithecine species (Clarke 1985a; Grine 1985; Leakey and Walker 1976; Pilbeam 1972; Pilbeam and Zwell 1972; Robinson 1954a, 1955,1961, 1963a, 1963b; Zihlman 1985), is <u>when</u> man became that specialist in culture. When did it become impossible for more than one biological hominid species to exist at one time?

The proponents of the single-species hypothesis argue that tool-use marked the time when man became dependent on culture and displaced all other hominid species (Wolpoff

1968, 1971:606-608). Others argue that tool-use is not man's niche, that tool-use is separate from, and precedes, man's dependence on culture adaptation (Lancaster 1968; Washburn 1960). Man's niche is dependence on cultural adaptation, and it was not until this occurred that all but one hominid species became extinct. Tool-use marks the beginning of, the transition to, culturally-dependent man, generally considered to be *Homo erectus*. As Hall stated:

> Instead it is reasonable to hypothesize that the early hominid species coexisted in Africa for several millions of years, avoiding competition with each other by seeking different kinds of prey and hybridizing too seldom to affect their individual integrity. Maintenance of two species of hominids could continue only so long as the niches of each remained well-defined and relatively narrow. With the evolution of *Homo*, probably in some peripheral population of australopithecines, the hominid niche broadened and absorbed the ecological styles of both hominids (1977:529).

Ernst Mayr summed up what he believed was the reason for the existence of only one species of *Homo*:

> It seems to me that the reason is man's great ecological diversity. Man has, so to speak, specialized in despecialization. Man occupies more different ecological niches than any known animal. If the single species man occupies successfully all the niches that are open for a *Homo*-like creature, it is obvious that he cannot speciate. This conforms strictly to Gause's Rule [The Competitive Exclusion Principle] (1950:116).

CHAPTER FOUR

A MODEL OF AUSTRALOPITHECINE RADIATION

> Living creatures press up against all barriers; they fill every possible niche all the world over. ...We see life persistent and intrusive spreading everywhere, insinuating itself, adapting itself, resisting everything, defying everything, surviving everything.
>
> - Sir John Arthur Thomson, 1920

The time is 5.5 million years ago, the place is what will eventually be named the Great Rift Valley in what will be East Africa. Among the many animals and plants, some familiar and some strange, is a small, bipedal ape. There are not many of them, they are still something of a rarity. But they are a tenacious group of apes. As the great forests of the Miocene shrank, breaking up into scattered islands surrounded by the sea of grass, the apes declined in numbers. Monkeys proliferated, and became the dominant primate life form. The apes became relics, a few species surviving in the forests. Except for one species which adapted to a new niche, by giving up the forests and taking up life in the bush and savannah, exploiting the mosaic of environments in the Great Rift Valley.

By 5.5 million years, this ape, this hominid we call an australopithecine, had adapted to the new environment. It

would eat anything it could get in its mouth and that did not poison it outright. It was bipedal, efficiently traversing the ground between patches of food, water and security cover. It had long arms for it still exploited the trees for food and protection. It lived in groups, a part of its primate heritage: it was an intensely social animal, and an intelligent one.

Over the next several million years, it increased in numbers and occupied the area from Ethiopia to South Africa, at least this is where its fossil remains have, so far, been found. As they spread southward, through what is now Mozambique, Malawi, Zambia, Zimbabwe and the Union of South Africa, they encountered different environments. The australopithecines avoided the dense tropical rain forest and the arid sands of the Kalahari, keeping to those environments similar to the ones they occupied. The cumulative change, though, was important.

The East African Rift Valley is a landscape rich in small environments--lake, river, marsh, gallery forest, savannah, volcanoes etc. The climate is generally warm to hot, the days are essentially the same length throughout the year. The only seasonality is because of the rain. Close to the equator, the rain comes at two distinct periods of the year--the long rains and the short rains, separated by a long dry season and a short dry season. Not surprisingly, this has its effects on the flora and fauna of the region.

They have had to adapt to extended periods of drought and heat.

The veldt of South Africa is a landscape of large areas of similar environments. The climate is definitely seasonal, not because of the rainfall pattern but because of the increasing distance from the equator. East Africa is equatorial; South Africa is in the temperate latitudes. The days vary in length, short and cool in the winter and long and hot in the summer. The flora and fauna adapted to this by growing in the summer and becoming dormant in the winter.

Not all the changes to which the australopithecines had to adapt are due to their increasing geographic range. There were global changes occurring simultaneously. There is evidence that the Pliocene was a period of increasing seasonality, with an increase in the mean temperature differential between the equator and the poles, and a decrease in rainfall, although this may have been partly due to the increasing seasonality that caused rainfall to be concentrated in definite periods, leaving other periods without rain.

The australopithecines adapted and survived for several million years. The earliest known australopithecine from South Africa is *Australopithecus africanus*, dating in the 2 to 3 million year range. This gracile form was beginning to show the physical changes that would characterize its descendants--*A. robustus*. It was larger than the earlier East

African forms, partly as a response to the cooler temperatures of the veldt. Its cheek teeth were becoming enlarged, also its brain was larger as it relied increasingly on problem-solving ability and memory to survive.

The robust forms had very large molars, reduced anterior teeth and a skull well adapted to chewing (extensive areas for muscle attachment, stronger facial bones, reduced muzzle). More and more plants had adapted to the cool season by developing tubers for energy storage (Coursey 1973), and the australopithecines had learned to exploit this food source. This is not to say that they ignored everything but vegetable foods. Lizards, insects, infant mammals, grubs, fledglings and carrion would have formed part of the australopithecine diet, along with nuts, fruits, berries, leaves and other edibles such as honey and bone marrow. However, during the winter, the lean season, roots and tubers would have formed the mainstay of the diet (Coursey 1973, Hatley and Kappelman 1980), teeth and jaws that could efficiently masticate these foods would have been of great adaptive value. It does not matter much how well you live during the best times of the year if you cannot survive the hard times. The robust australopithecines remained omnivorous, but with adaptations to deal with tough fibrous vegetable matter. The environment in South Africa was largely homogeneous and so was the population of robust australopithecines. They had no serious competition; they

were the only hominids (the only apes also) for several million years. Then a more evolved hominid arrived--*Homo*. *Homo* came bearing culture, carrying it in a larger brain. The australopithecines were not able to compete. Their behavior was not flexible enough, and they could not, biologically, adapt to a new niche that *Homo* could not occupy, at least not fast enough. *Homo* had an adaptive niche broad enough to cover any niche *Australopithecus* could possibly occupy or adapt to; there was, literally, no room for *Australopithecus*. He disappeared, extinct.

The situation in East Africa was different from that in South Africa. The landscape was a mosaic of habitats, potential niches. These micro-habitats are in constant flux; the Great Rift Valley was, and is, a tectonically active, dynamic environment. Lakes changed, not just seasonally, but over long spans of time. The lakes changed size, shifted their locations, disappeared, reappeared, became brackish or fresh. Rivers reversed their flow, or dried up. Volcanos erupted, temporarily or permanently altering vast areas, then the volcanos eroded away. Forests appeared on wetter escarpments of the evolving rift valley and disappeared when higher hills rose and cut off the moisture. It was a turbulent landscape, although many of the changes were on a time scale such that even tens of generations of australopithecines would not have noticed any difference.

The oldest known East African australopithecines, dating around 3.4 millions year ago, are the ones called *Australopithecus afarensis*. These afarines are a more primitive hominid than the gracile forms from South Africa. They are, also, 0.5 to 1 million years older. The afarines may not be ancestral to all the australopithecines, but they probably closely resemble that ancestral stock (the "basal hominid"). In the heterogeneous environment of East Africa, the populations of afarines became a heterogeneous collection of adaptive life styles.

At 2.5 million years ago, we have evidence (in the form of KNM-WT 17000) of a definite trend on the part of one population toward an econiche similar to the one to which the South African robust forms were going to adapt. Possibly the early East African robust forms contributed, genetically, to that trend in South Africa. The South African robusts never developed to the hyper-robust extreme that the East African forms did (by 1.75 million years ago), in the shape of *A. boisei*. They did not need to; it was only the East African robust forms that had to compete with a significantly different adaptive lifestyle of another australopithecine population.

The hyper-robust australopithecines were at one end of a spectrum of adaptive lifestyles. Possibly, they were spending more time on the savannah and in the bush, exploiting the roots, tubers and other vegetable matter in those

environments, getting their water more frequently from streams and waterholes, than from lakes and rivers. Some of their adaptations were learned behaviors, but much of it was physical adaptation, genetic. The evidence is in their teeth and skulls.

At the other end of this spectrum of adaptations, was a population that did not develop the cranio-dental modifications of a more vegetarian lifestyle. This population remained more generalized, more omnivorous in its eating habits--perhaps, because life was easier. Possibly they lived along the large lakes and permanent rivers. They did not have to depend so much on tough, fibrous tubers and roots during the dry seasons and droughts; there was enough other food available. These populations probably lived in larger and more socially active groups than did the hyper-robust forms. There would have been a premium placed on those individuals more socially adept, more quick-witted, more capable of learning. Within this population, behavior patterns common to all the australopithecines were elaborated, intensified, and passed on to the next generation. They became increasingly dependent on learning to adapt to conditions, rather than upon evolving physical adaptations.

In the beginning, it was only a marginally "better" adaptation, at least compared to being physically generalized and not very intelligent. Initially, robust populations were more successful because they were better adapted.

Learned behavior could be forgotten or learned incorrectly, tools could be lost, and raw material unobtainable. The teeth, jaws, and muscles were always present. Nonetheless, that odd little population of unspecialized hominids persisted; its adaptations did work, after a fashion and, as time went on, they worked even better. Nut-cracking teeth were useful, but ultimately, they narrowed one's future options. A hand that (with the coordination of eye and brain) could wield a nut-cracking stone could also wield a meat-slicing flake. The capacity for cultural adaptation was a specialization of unlimited options. When some hominid figured out how to put a sharp edge on a round pebble, the door was opened to those options. The population of physically generalized hominids began to expand their econiche, usurping the econiches of the other australopithecines. The robust australopithecines adapted the only way they could--physically. They became hyper-robust, specializing in a narrow portion of their econiche. But, that only served to stave off their eventual extinction, whereas that generalized hominid, now *Homo erectus*, spread throughout the Old World land mass, except for those areas too cold to endure without fire. But that would come, too.

CHAPTER FIVE

THE FOSSILS

> The truth is that man is a solitary and peculiar development.
>
> -Loren Eiseley (1957:158)

The fossils of the Plio-Pleistocene hominids come primarily from two geographic areas: southern and eastern Africa (see Figure 2 for a map of Africa with the locations of the fossil hominid sites).

The South African sites are Taung, Sterkfontein, Swartkrans, Kromdraai and Makapansgat (Howell 1955). All these sites are limestone deposits, in what were once caves. These caves were originally solution cavities, formed beneath the surface of the earth. Over the years, carbonate-rich water, passing through the cavities, filled them with dripstone. In some of these cavities, further erosion formed passages that opened to the surface, then bones were washed into the cave and buried in the dripstone (Brain 1981). The caves were not occupation sites like the caves of the Dordogne. When they were first discovered, it was assumed that they were the living sites of the australopithecines, and a number of theories were based on this assumption (Ardrey 1961; Dart 1926, 1949, 1953, 1959a, 1962a, 1971; Thompson

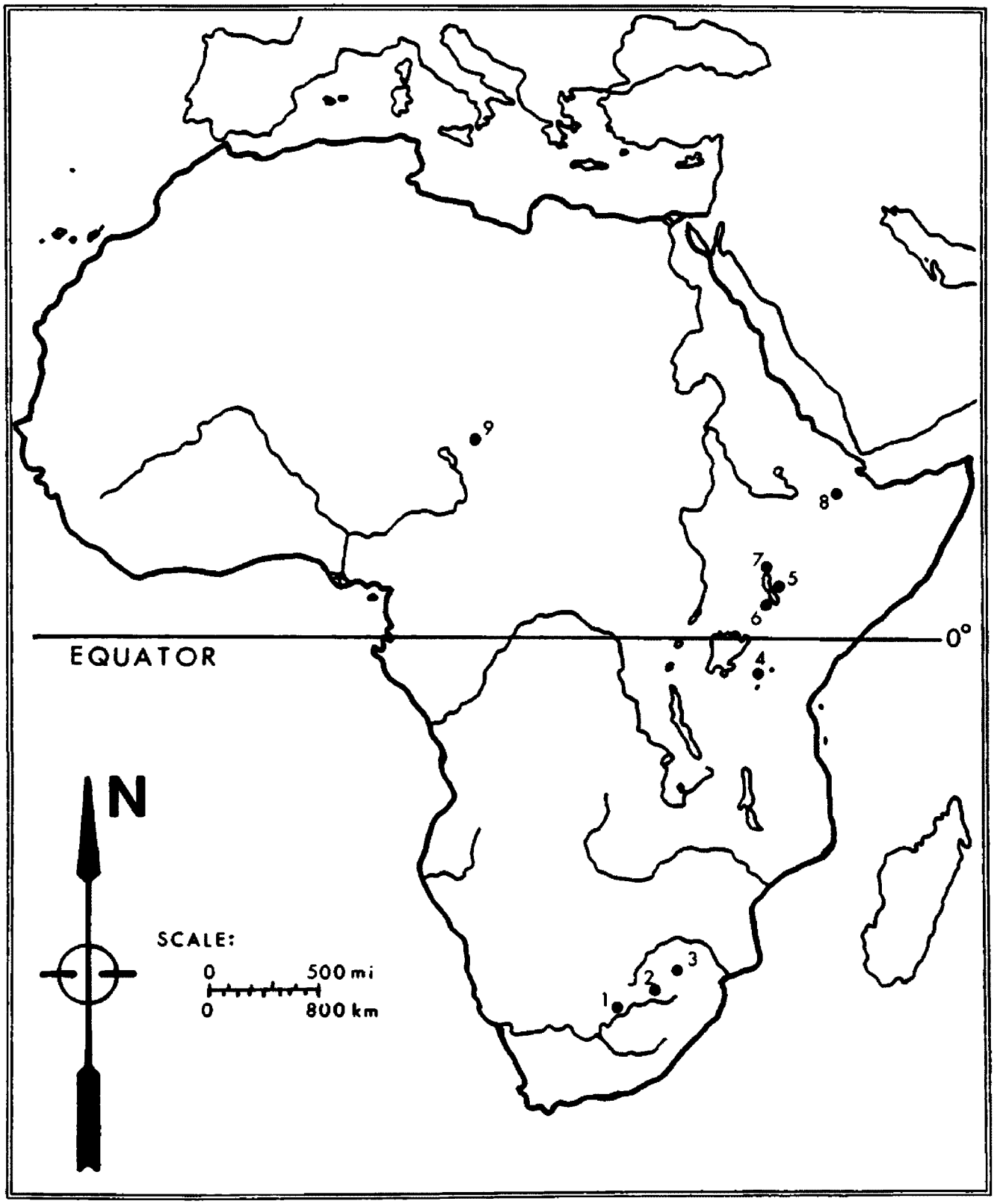

FIGURE 2. Map of Africa showing locations of fossil hominid sites mentioned in the text. 1) Taung, 2) Sterkfontein, Swartkrans, and Kromdraai, 3)Makapansgat, 4) Olduvai and Laetoli, 5) Koobi Fora (East Rudolf), 6) West Turkana, 7) Omo, 8) Middle Awash and Hadar, 9) Koro Toro (Chad) (Adapted from Cooke 1963)

1975, 1976). Further work has done much to elucidate the complex history of these deposits (Brain 1981), and to demonstrate that the bones were secondarily deposited in the caves by natural forces, not by human activity (Brain 1981).

The deposit at Taung was the site of the first australopithecine find (Dart 1925). The only hominid fossil found at Taung (also called Buxton-Norlim) was the skull of a child, the type specimen of *A. africanus*. It was found in a limestone breccia that was being mined. Unfortunately, this commercial activity has destroyed the site and the context of the fossil is poorly known (Dart 1926). The date of the deposit is subject to much argument; estimates of its age vary from 0.87 M. Y. A. to 2.5 to 3.0 M. Y. A. (Butzer, Todd, Blumenberg, and Tuttle 1974; Howell 1978; Lewin 1985). Most of the age estimates are around 1.0 to 2.0 M. Y. A. (Vogel 1985), and general consensus seems to be that the site is about 1.0 to 2.0 M. Y. A., most likely nearer 1.0 M. Y. A. (Day 1986). No tools were found in the deposit (Day 1986).

Sterkfontein is the site at which the first adult australopithecine was found (Broom 1936). The cave deposits that contain the hominid bones consist of two members: Member 4 and Member 5. Member 4 is the older deposit lying below Member 5 (Brain 1981). Based on faunal analysis the best estimates for the date of Member 4 is 2.4 to 2.8 M. Y. A., and for Member 5 about 1.5 to 1.8 M. Y. A. (Day 1986).

A lower deposit, below Member 4 may date to 3.26 M. Y. A. This deposit does not contain hominid bones. All the hominid bones from Member 4 have been referred to *A. africanus* (Howell 1978), and include such finds as the nearly complete skull, known by its museum accession number as STS 5 (Sterkfontein Type Site 5), or Mrs. Ples, and a pelvis, STS 15, along with many teeth. Member 5 contains stone tools and hominid fossils which have been referred to *Homo habilis* (Clarke 1985b; Hughes and Tobias 1977), and several that might be *A. robustus* (Day 1986). The geology of the Sterkfontein cave is complex (Brain 1985) and much of the infilling has been removed and burned for lime. This has, as in all of the other South African sites, made determining the context of the fossils complicated. Typologically, the stone tools are either Late Oldowan or Early African Acheulean (Clarke 1985b; Day 1986).

The Makapansgat Limeworks Deposits have also yielded fossils (Boné and Dart 1955; Dart 1948a, 1948b, 1959b, 1962b, 1962c) which are now generally attributed to *A. africanus* (Day 1986). When the fossils were originally found, Raymond Dart (1948a) believed he had evidence of the use of fire (hence the original name of "A. prometheus") and the use of tools (his osteodontokeratic culture). The evidence for the use of fire and tools has not withstood further examination (Bilsborough 1971; Brain 1981; Hill 1976; Shipman and Phillips 1976; Shipman and Phillips-

Conroy 1977). Makapansgat, which has been dated by palaeomagnetic studies and faunal analysis, is probably the oldest of the South African australopithecine sites. Most of the hominid remains come from a deposit that is greater than 2.9 M. Y. A., and perhaps as old as 3.06 M. Y. A., but younger than 3.3 M. Y. A. (Day 1986; Howell 1978). A deposit above the main fossil layer is slightly younger, and the entire Makapansgat deposit may range from 2.5 to 3.0 M. Y. A. (Day 1986; Tattersall, Delson, and van Couvering 1988), although an attempt to date the site by paleomagnetism yielded an older range of dates: 2.8 to 3.7 M. Y. A. (Brock, McFadden, and Partridge 1977).

The first of the fossils attributed to *A. robustus* were found at Kromdraai (Broom 1938). Almost all the specimens have been found out of context, although it has been possible to determine the source of the bones. Only one definite stone artifact and several possible artifacts have been recovered from the site (Day 1986). Dating the Kromdraai deposits has been difficult, but a date of 1 to 2 M. Y. A. (probably 1.0 to 1.2 M. Y. A.) seems to be generally accepted (Day 1986; Howell 1978).

Most of the *A. robustus* fossils have come from Swartkrans. These are referred to as "A. crassidens" by some people (Grine 1985). It is also from Swartkrans that the fossils originally name "Telanthropus capensis" came (Broom and Robinson 1950).

Like Sterkfontein, the Swartkrans fossils are from two different layers, now termed Member 1 and Member 2 (Brain 1981). All the fossils attributed to *A. robustus* are from Member 1, which is the lower and older stratum (Day 1986; Howell 1978). It has been dated at 1.5 to 2.0 M. Y. A. (Tattersall, Delson,and van Couvering 1988). Member 2, dated at 0.5 M. Y. A. to the present, contains the fossils, formerly attributed to "T. capensis," now considered to be *H. erectus* (Brain 1985; Howell 1978; Olson 1978; Tobias 1973, 1985b), although it has been suggested (Corruccini and McHenry 1980; Groves and Mazák 1975; Leakey, Tobias, and Napier 1964) that they are *H. habilis*. Stone tools that appear to be of Oldowan type have been recovered from the breccia dumps, although it has been difficult to determine their stratigraphic position within the cave. In Member 1, some bone fragments that have been interpreted as digging tools have been recovered (Day 1986).

The situation in eastern Africa is different, more complicated, and far more informative. Not one of the fossil sites is a cave, and some are believed to be living floors. The first of the australopithecines found in East Africa was found on what some have argued was living floor (Isaac 1978a, 1978b; Hewes 1961; Potts 1984, 1985; Read-Martin and Read 1976; Shipman and Phillips 1976). The question is still unresolved (Binford 1981, 1984, 1985). At Olduvai, the hominid fossils which are of concern to us here

all come from Bed I or Bed II. The fossils from Bed I, the oldest level, have been attributed to either *Australopithecus* (*A. robustus* or *A. boisei*) or *Homo habilis* (Leakey, Clarke, and Leakey 1971), associated with Oldowan tools. All the fossils except one from Bed II have been attributed to *Homo erectus* (Rightmire 1979) and are associated with Acheulean tools. The exception, OH (Olduvai Hominid) 20, a neck of a femur, has been referred to *A. boisei* until further comparative material is available (Day 1986). It is a surface find and is either lower Bed II or upper Bed I. Olduvai has been datable by potassium-argon (K/Ar), and Bed I is now dated at 2.1 to 1.7 M. Y. A. Bed II is dated at 1.7 to 1.15 M. Y. A. (Day 1986; Rightmire 1979).

Laetoli, which is near Olduvai, is more famous for its footprints (Hay and Leakey 1982; Leakey and Hay 1979), than for its fossils, but a number of hominid fossils have been found there (White 1976, 1980). The older Laetolil Beds (the site is known as Laetoli, the geologic formations are called Laetolil) have yielded fossils of a gracile australopithecine which Johanson, White and Coppens (1978) designated as the lectotype of *A. afarensis*. The Laetolil Beds are older than Bed I at Olduvai, and are dated at 3.6 to 3.75 M. Y. A. (Harris 1985; White 1976). Some of the fossils are of *Homo sapiens*, but they are from the younger Upper Ngaloba Beds, which is tentatively dated at 120,000 ±30,000 B. P. (Day 1986).

In Kenya, most of the fossils of Plio-Pleistocene hominids have come from the region around Koobi Fora. The fossils are numerous (Brown, Harris, Leakey, and Walker 1985; Day and Leakey 1973, 1974; Day, Leakey, Walker, and Wood 1975, 1976; Leakey 1972; Leakey, Mungai, and Walker 1971; Leakey and Walker 1973, 1985, 1988; Leakey and Wood 1973, 1974), and more continue to be found each year. Most of the remains are fragmentary, and our knowledge of differences between the various australopithecines and early *Homo* is too limited to allow us to make accurate specific attributions or even, in some cases, generic. Because of this, it is the policy of the Koobi Fora Research Project (Day 1986) not to make specific attribution of the fossils, except in those few cases (KNM-ER (Kenya National Museum-East Rudolf) 3733 and KNM-WT (West Turkana) 15000) where there is little doubt (Brown, Harris, Leakey, and Walker 1985; Day, Leakey, Walker, and Wood 1975). Most of the fossil remains from Koobi Fora have, therefore, been attributed to either *Homo* sp. indet. (species indeterminate) or *Australopithecus* sp. indet. In the few instances where it has been considered possible to refer a fossil to a species, the species have been either *Homo erectus* or *A. boisei* (Brown, Harris, Leakey, and Walker 1985; Day, Leakey, Walker, and Wood 1975; Leakey and Walker 1988). Some anthropologists have also made claims for the presence of *H. habilis* among the Koobi Fora fossils (Campbell 1988; Howell

1978). Although the Koobi Fora deposits cover an age range of 4.1 to <1.39 M. Y. A. (Day 1986), the hominid-bearing deposits are more limited in age. The geologic formations in which fossils have been found in the Koobi Fora region are: the Chari, Okote, and the KBS (Kay Behrensmeyer Site) members. These formations range in age from less than 1.4 M. Y. A. to less than 1.8 M. Y. A. (Day 1986).

Across the jade green waters of Lake Turkana was found the very complete remains of a young male *Homo erectus* (KNM-WT 15000) (Brown, Harris, Leakey, and Walker 1985). It is dated about 1.6 M. Y. A. North of Koobi Fora, in Ethiopia, is the basin of the Omo River. As at Koobi Fora, and most everywhere else for that matter, the fossils are fragmentary. They have been described as *A. africanus*, *A. boisei*, and *H. erectus* (Day 1986; Howell 1978; Leakey and Walker 1988; Walker, Leakey, Harris, and Brown 1986). In some of the younger deposits (the Kibish Formation, 3,100-130,000 years B. P.) are fossils of *H. sapiens* (Day 1986). The Omo deposits have been dated by potassium-argon, and the entire sequence is from 1.34 to 3.3 M. Y. A. (Day 1986). The *A. africanus* fossils are from the lower and older units. They are overlain by deposits with the fossils attributed to *A. boisei*, along with a few that are attributed to *H. habilis* (Day 1986; Howell 1978). Above these are some cranial fragments that some scholars attribute to *H. erectus* (Day 1986). Also in Ethiopia are the Hadar and the Middle Awash

deposits. The Middle Awash fossils consist of a femoral fragment and a frontal fragment (Day 1986); dated to 3.5 to 4.0 M. Y. A. and are among the oldest known australopithecine fossils (Day 1986). The femur is the oldest evidence of bipedalism.

The Hadar fossils, including AL (Afar Locality) 288-1, were originally thought to fall into three groups, one a gracile australopithecine, the second a robust australopithecine, and the third is considered to have affinities to the hominine material from Java (Day 1986). But Johanson, White and Coppens (1978) have argued that they represent a new species of australopithecine, *A. afarensis*. The naming of the species (Hinrichsen 1978; Johanson, White and Coppens 1978) has been beset with nomenclatural and procedural problems (Bielicki 1966; Day, Leakey, and Olson 1980; Ferguson 1983; Johanson and White 1980; Leakey and Walker 1980), along with much contention as to the validity of the species. The arguments vary from whether *A. afarensis* is different from the other known and previously named australopithecine species to whether *A. afarensis* is composed of several species, not one (Ferguson 1983; Zihlman 1985). Hadar has been dated at 3.3 M. Y. A. (Walter and Aronson 1982).

Fossils of Plio-Pleistocene hominids have been found in other locations, but the finds are generally small and fragmentary. The fossils from two of those sites are of

particular interest here: Koro Toro in Chad and Sangiran, Java. The fossil from Chad was originally name "Tchadanthropus uxoris" (Coppens 1966), but now is usually considered to be a gracile australopithecine. There have been some who believed it to be *H. habilis* or *H. erectus* (Howell 1978). E. L. Simons (1967) said it is fragmentary and too badly eroded to be certain of its affinities beyond being hominid. It could be anything from *Australopithecus* sp. to *Homo* sp.

The fossil mandibles from Sangiran were originally named "Meganthropus paleojavanicus," (von Koenigswald 1945). J. T. Robinson (1953a, 1955, 1963b) attributed them to "Paranthropus paleojavanicus," an Asian robust australopithecine. Others consider them to be *Homo erectus* (Pope and Cronin 1984). The Djetis Beds, in which the fossils are found, have been dated (K/Ar) at 1.9 ± 0.04 M. Y. A. (Jacob 1972). However, the age of the fossils is uncertain (Pope and Cronin 1984) and I shall not consider them further, as I am inclined to agree with Pope and Cronin. I view the Asian fossils as an early *H. erectus*, indicative of the rapid spread of *H. erectus* out of Africa.

In general, the fossil evidence indicates the appearance of a population of hominids in East Africa before 4 M. Y. A., possibly even as early as 5.0 to 5.5 M. Y. A., if the fossils found at Lothagam (Howell 1978) and Baringo (Pickford, Johanson, Lovejoy, White, and Aronson 1983) are

australopithecines. This stem population diverged and expanded its range over the next several million years. In South Africa, the australopithecines appeared around 3.0 to 2.5 M. Y. A. and existed until around 1.0 M. Y. A. There were two populations, an earlier "gracile" population, and a later "robust" population. The robust population coexisted, at least in its later stage, with a population of *Homo* (Leakey 1973).

In eastern Africa, the stem hominid population evolved into two populations: a "gracile" population and a "hyper-robust" population. Depending upon the taxonomy chosen these populations may be either: *Homo* and *Australopithecus*, or *Australopithecus* and *Paranthropus* (Robinson 1972). These two populations coexisted over several million years. The hyper-robust population eventually became extinct and the gracile population evolved into *Homo erectus* and spreading throughout the Old World, eventually became *Homo sapiens*.

CHAPTER SIX

PALEOENVIRONMENTS

> Always, organism and environment are interacting systems, not contrasts.
>
> -Marston Bates (1960:553)

When the hominid-bearing deposits of South Africa were first discovered and for a time thereafter, the dominant concept in African geology was the Pluvial Theory (Howell 1955). Basically, the Pluvial Theory postulated an alternating sequence of periods when rainfall was higher than at the present time. The sequence was thought to be analogous to, and synchronic with the Ice Ages of the northern hemisphere. There were discussions whether the pluvials occurred at the same time as the glacials or whether they occurred at the same time as the interglacials. Some geologists argued that the growth of the glaciers meant increased worldwide rainfall, and the pluvials were synchronous with the glacial periods. Others argued that the glaciers "locked up" much of the world's water and the glacial periods were times of drought in the rest of the world. It was not until the glaciers melted that moisture was available and rainfall increased around the world, and the pluvials were synchronous with the interglacial periods. The timing

and number of African pluvials could not be ascertained and, eventually, the lack of evidence for the pluvial theory led to it being discarded as an explanation for African paleoclimates (Deacon 1983; Flint 1959).

Current ideas (for example: Bishop 1963; Boaz 1977; Bonnefille 1985; Brain 1987; Butzer 1971; Cadman and Rayner 1989; Cerling, Hay, and O'Neil 1977; Deacon 1983; Evans, Van Couvering, and Andrews 1981; Harris 1985; Hill 1987; Horowitz 1975; Laporte and Zihlman 1983; Leakey 1963; Partridge 1985b; Williamson 1985; Vrba 1974, 1975, 1985a, 1985b) about the African paleoclimates are that, over the past few million years, climates have not varied much from the current conditions. The Miocene climate is believed to have been wetter than now, with more forests (Bonnefille 1985; Evans, Van Couvering, and Andrews 1981; Flint 1959; Laporte and Zihlman 1983; Yemane, Bonnefille, and Faure 1985). By the end of the Miocene the climate was becoming drier, and the forests were becoming smaller. It is believed that a part of this change was due to an increase in seasonality and an increase in the mean temperature difference between the low latitudes and high latitudes. Increasing seasonality means that the difference between seasons became more pronounced, winters were colder and summers hotter, dry seasons drier and wet seasons rainier. The increase in the mean temperature differential between low latitudes and high latitudes meant that the

difference in the average yearly mean temperatures in the topics, the temperate and the polar zones became greater. The tropics probably did not get much hotter, but the poles became much colder. The temperate latitudes became, on the average, cooler. These were worldwide changes (Hill 1987; Laporte and Zihlman 1983; Williamson 1985). The usual expression is that the climate of the earth was beginning its long, downward slide into the Ice Age.

Almost 5.0 to 5.5 M. Y. A. the Mediterranean Sea dried up (Hsü, Montadert, Bernoulli, Cita, Erickson, Garrison, Kidd, Mèlierés, Müller, and Wright 1977), which had quite an effect on the circum-Mediterranean area. Thick beds of salt layer the floor of the Mediterranean Sea, deposited when it dried up, this led to the term "salinity crisis" to refer to the event. As Hsü, et al. stated (1977:402): "The salinity crisis appears to have induced a continued change towards a cooler and more arid climate on the circum-Mediterranean." The Antarctic ice cap expanded and the ice sheet over the Arctic Ocean may have formed then, possibly caused by the salinity crisis. The aridity probably led to an expansion of savannah vegetations, and a selective advantage for drought-resistent plants. Although the salinity crisis had a severe effect locally, just how much of an effect it had on other regions is still uncertain (Hill 1987) and, as far as this thesis is concerned, largely irrelevant. The salinity crisis occurred at the end of the Miocene and,

although it may have been a factor in the appearance of the australopithecines (Hsü, et al. 1977), it had little or no effect during the middle to late Pliocene, the time of the australopithecine radiation and the concern of this thesis. More relevant, is the evidence that the downward trend in temperature became steeper about 2.5 M. Y. A. (Brain 1987; Vrba 1985a, 1985b). Previously, the rate of change had been very gradual, but after 2.5 M. Y. A., the rate of change was greater.

The South African caves all lie within approximately the same area: the high veldt of South Africa (Howell 1955). The present environment is roughly the same as it was at the time the caves were being filled with sediment and bones. Present climate is also roughly similar to what it was then, a little wetter at times, a little drier at other times, but, roughly similar. It was once believed that the robust australopithecines lived in South Africa during the pluvials, and the gracile australopithecines lived in South Africa during the interpluvials (Howell 1955). Apparently, the gracile and robust australopithecines populations alternated living in South Africa, as the pluvials and interpluvials alternated. The gracile and robust australopithecines are not correlated to any particular environment (wetter or drier) (at least not in the sense as scholars once believed, see Cadman and Rayner 1989), rather they are correlated with age of the deposit.

Gracile australopithecines are found in older deposits (at which time the climate may have been rainier than at present time) and the robust australopithecines are found in the younger deposits (at which time the climate may have been drier than during the earlier time of the gracile australopithecines).

All the cave sites in the South African veldt are at an altitude of about 4,000 feet, or more, and at a latitude of about 30°S. The country is gently rolling and has little relief. Rainfall averages 25 to 30 inches in the eastern part of the veldt, in the western veldt rainfall averages closer to 15 inches. Around Taung the rainfall averages around five inches (Dart 1926). What few trees and bushes grow on the veldt, grow primarily along the small watercourses (Howell 1955). This plateau-like region of the caves is bounded on the south by the Drakensberg Mountains, which form an escarpment between the plateau to the north and the coastal plains to the south and east. To the west the veldt fades into the Kalahari Desert, to the north and northeast it crosses the Zambezi River and merges with the basin of the Zaire (formerly the Congo) River basin with its forest or the lakes of the Great Rift Valley.

Although the veldt lies at a latitude similar to the southern United States, it is climatically different. The Drakensberg Mountains block the warm moist air off the Indian Ocean and the veldt is semi-arid. Aridity increasing

toward the west. Because of its altitude the veldt can become relatively cold, especially during the nights of the southern winter. Lying so far south of the equator it has one dry season alternating with one rainy season each year. Rains fall mainly in the summer, the winters are cool and dry.

Between 3.0 M. Y. A. and 2.0 M. Y. A., the vegetation changed from a bush-and-tree cover to more open grasslands (Vrba 1974, 1975, 1985a, 1985b). This shift in vegetation may not be due to an absolute decrease in total rainfall as much as to a change in the timing of the rainfall. Rain spread evenly throughout the year promotes the growth of bushes and trees, whereas the same amount of rain concentrated in shorter periods of time (rainy seasons) with periods of drought (dry seasons) between, promotes drought-tolerant grasses and herbaceous plants (Hatley and Kappelman 1980).

Over the time span of the cave deposits, the plant cover shifted from a bush-and-tree cover to a grass-and-bush environment. The fauna changed too; those animals that preferred more open conditions became more common, and those of the forest and dense bush became rarer.

The South African veldt was, and still is, comprised of vast expanses of similar environment. There was some variation, patches of different environment; but these microhabitats were small and scattered throughout the vast expanse of bush or grassland.

The environment in eastern Africa is different, it is a mosaic of micro-habitats, the Rift Valley in particular. It is true that much of eastern Africa, that is, Tanzania, Kenya, Uganda, Rwanda, Burundi, Sudan, Somalia, and Ethiopia, not just the area known as British East Africa, is large expanses of similar environments. The Serengeti, the Chalbi Desert, are examples of this. The Rift Valley, and it can be spoken of as THE Rift Valley, is different. The Rift Valley runs through much of eastern Africa (see Figure 3), and it is geologically unique and ecologically an ever-changing mosaic of micro-habitats. The Rift Valley is tectonically active, a land of earthquakes and volcanoes. It is bounded by escarpments, that in some places rise sheer from the valley floor as a single wall, in others as a series of giant steps, either rising as much as 1,000 meters or more. The floor of the Rift Valley is often cut by transverse faults, and the drainage pattern within the rift is constantly being disturbed. A river will flow in one direction for many years, until an earthquake causes a fault block to shift and dam or reverse the flow. A lake or marsh would form where the river was blocked. Trees would grow along the margins of lakes and rivers. Large rivers, like the ancestral Omo or the present Ewaso Ngiro have dense stands of trees along their banks. Narrow ribbons of tropical rain forest, maybe 100 meters wide, line the rivers. Beyond the narrow ribbon is the thorn bush, acacia, and the

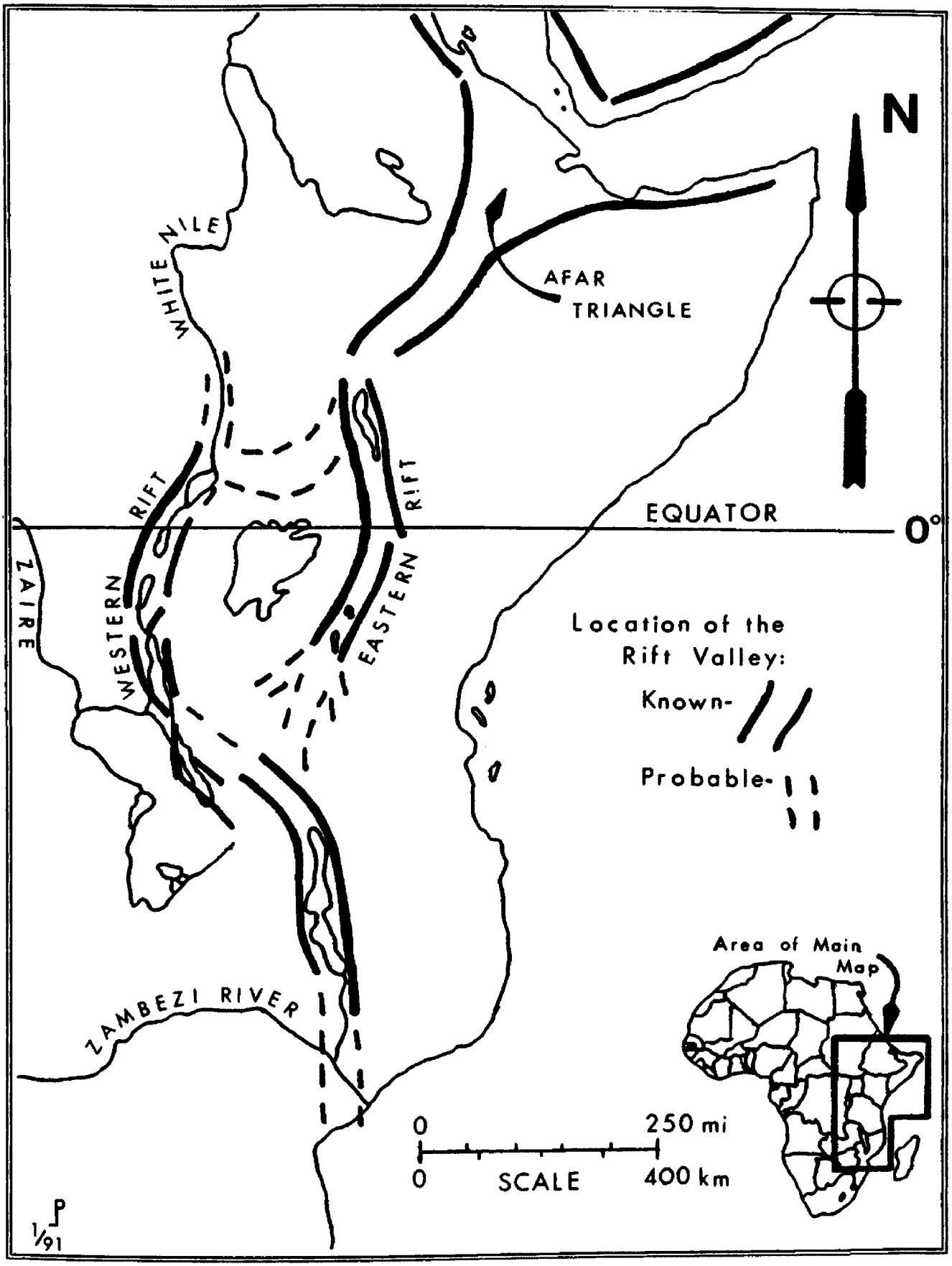

FIGURE 3. Map of the Great Rift Valley

stony wastes of the surrounding desert. The Rift Valley contains numerous habitats: soda lakes, fresh-water lakes, ephemeral streams, rivers, deserts, thorn bush, grass lands, springs, gallery forest, acacia woodland, forested mountain slopes. All of these are jumbled together, occasionally reshuffled by the same geologic forces that formed the rift.

The yearly climatic cycle of the equatorial Rift Valley is marked by variations in rainfall. Near the equator the day length varies by only a few minutes a day, and the range in temperature is not great. Rainfall, or the lack of it, is the dominant environmental factor. Near the equator, there are two rainy seasons and two dry seasons each year. In southern Kenya and Uganda, the "long rains" are from March to June, then there is a dry season until about October when the short rains begin and continue to December. In Tanzania, the long rains are from April to May, and the short rains are from November to December. As one moves further from the equator, both north and south, the pattern of two rainy seasons (called a double maximum) changes to just one rainy season alternating with one dry season (in sub-Saharan Africa the rain occurs in the summer and therefore it is called a summer maximum). In Malawi, the rainy season is from October to April and, in Zambia and Mozambique, from November to April. In the southern Sudan, which is north of the equator, the rains fall from April to November, when they fall. Outside the equatorial rain forests

and a few unique habitats (i.e. the cloud forests of the Ruwenzori Mountains), drought is the critical environmental factor. All organisms must have some means of surviving the long dry season that occurs each year. If the rains fail, as the short rains sometimes do, it can be a very long, long dry season. In the same way that in the polar regions, cold and darkness dominate the lives of plants and animals, heat and dryness dominate their lives in the tropics.

The environment of eastern Africa during the Plio-Pleistocene was, like South Africa, similar to the present day environment. There were some differences though. There may have been more rain in the Rift Valley until 1.8 to 2.0 M. Y. A. in the Lake Turkana region (and 0.5 to 0.6 M. Y. R. in the Olduvai Gorge region), when there is evidence that there was a dramatic decrease in rainfall (Cerling, Hay, and O'Neil 1977). The region of the Middle Awash Valley and the Afar Depression in Ethiopia, was not as desolate during the Pliocene as it is now (Kalb, Jolly, Oswald, and Whitehead 1984). Other than the volcanoes of the Virunga Mountains, along the Rwanda-Uganda border, there is essentially no volcanic activity in eastern Africa. The geology of the Rift Valley resembles a layer cake with sediments, volcanic flows and ash falls. The impression these alternating layers of volcanic sediments gives is one of continuous volcanic activity in the past, which has now ended. However, this is misleading. The deposits accumulated over

millions of years, and the episodes of volcanic activity are separated by hundreds, thousands, and hundreds of thousands of years. The volcanic activity was episodic, with long periods when there was little or no volcanic activity, like now. Almost certainly, the present period is just a lull before the next episode of vulcanism.

The geologic strata in eastern Africa, in which the hominids fossils have been found, are almost all fluvial, fluvial-lacustrine, and lacustrine deposits (Bishop and Pickford 1975; Boaz 1977; Leakey 1963). The major exception is Laetoli, which is a terrestrial deposit that is indicative of an open grassland with scattered trees (Harris 1985).

What is important about the Rift Valley is this habitat "patchiness," this dynamic collection of micro-habitats. Any organism that is sufficiently flexible in its diet and in its behavior could exploit this variety of habitats, never depending totally, or even significantly, on any one habitat. In a dynamic environment like the Rift Valley, total or near total dependence on one habitat could lead to extinction of at least a population, if not the species, when that habitat disappeared. Further, any organism that got only a part of its sustenance from any one habitat would not be competing seriously with other organisms that lived in that habitat.

CHAPTER SEVEN

THE ECOLOGICAL MODEL:

SOUTH AFRICA

> The study of human origins is an attempt to determine a historical sequence of events from inadequate data. It is evident to all that the data are inadequate at present. It is highly probable that they will always be inadequate, because they must remain ambiguous in the sense that they will be consistent with more than one possible interpretation. . .
>
> Our task, then, is to take inadequate data, to reject interpretations that definitely do not fit these data, and then judge the probability of the usually still multiple possible interpretations that remain.
>
> -G. G. Simpson (1950:55)

The process of fossilization has not been kind to the remains of our primate ancestors. On the other hand, considering the propensity of primates to live in habitats that are not conducive to fossilization, the fact the we have any primate fossils, at all, is an act of kindness of fossilization (please excuse the anthropomorphism). The first traces of hominids appear about 5.5 M. Y. A. (Howell 1978). But the first significant fossils (those that enable us to begin to reconstruct the organism) are younger, only 3.5 M. Y. A. old. The earliest hominid for which we have good evidence is the one that has been named *Australopithecus afarensis*

(Johanson, White and Coppens 1978). The fossils of these "afarines" are of a small, lightly built, bipedal animal. The muzzle is prognathic, the arms are relatively long and the brain is a little larger than might be expected for an ape of that size.

The afarines were already bipedal (Langdon 1985; McHenry and Temerin 1979), and for reasons beyond the scope of the present work. To me, bipedalism is the distinguishing trait that divides the australopithecines from their predecessors. The australopithecines were small-brained, bipedal hominids (*Homo* is a large-brained, bipedal hominid). The afarines were living in the woodlands, gallery forests and savannah of eastern Africa. It is not possible to reconstruct the lifestyle of these early australopithecines with much certainty, neither do we really know what kind of life their predecessors led. We do not even know what their predecessors were. However, it is possible to develop a plausible, if general, model of the afarine niche from what we now know. From this general model it will be possible to gain an idea of the selective pressures operating on the early australopithecines populations and an idea of adaptive trends (Peters 1979).

The afarines lived in eastern Africa around the lakes and rivers of the Rift Valley; probably the australopithecines were restricted by the availability of surface water. Modern humans have a need for water; our bodies use much

water to keep cool, and it has been postulated (Zhilman and Cohn 1988) that this increased physiologic need for water, and probably man's hairlessness, evolved at the time when the hominids began to adapt to life on the savannah. There are opinions to the contrary (i. e. Wheeler 1984), and the entire problem is a field for much speculation (Ebling 1985). The australopithecines were probably no more adapted to living in desert conditions than any other primate. They could not use areas that were so far from a source of surface water as to prevent them from returning frequently for water. Except for the constraint imposed by this need for water, the australopithecines could live nearly anywhere. They probably lived in areas outside of the Rift Valley; however, no fossils have been found there. Either the fossils have not been found or it is possible that fossiliferous deposits of sufficient age and the environment simply do not exist in these areas. The afarines living in the Rift Valley, were living in an area of high geologic activity and habitat diversity. If they had the behavioral flexibility needed, and the intelligence to learn how to exploit the resources in each different type of habitat, the afarines's bipedalism enabled them to exploit the different habitats. As I have pointed out above, the Rift Valley is a mosaic of micro-habitats. Each of these micro-habitats would have resources that could be used by these early hominids. The resources within each micro-habitat would be

capable of supporting a few animals for a short period of time, before being exhausted. A mobile omnivorous animal with a flexible behavior pattern and with the ability to learn, could effectively exploit these micro-habitats (Malone 1987). The major adaptive trends would be: 1) an increase in ability and efficiency in movement, 2) an increase in ability to process a wide range of foods (both plant and animal), 3) a flexible behavioral system, and 4) an increase in general intelligence.

The trend toward an increase in ability and efficiency in movement would be primarily expressed by morphologic improvements in the limbs, pelvis and spine. Although there are arguments about how efficiently bipedal the australopithecines were (Jungers 1982; Langdon 1985; Lovejoy, Heiple, and Burstein 1973; McHenry and Temerin 1979; Stern and Susman 1983; Susman, Stern, and Jungers 1985; Wolpoff 1983), the footprints at Laetoli indicate that they were at home on the ground and adequately adapted, morphologically, to bipedalism. The post-cranial anatomy of the australopithecines would not need to change much, if at all. Movement from one habitat to another would increase exposure to predators. Defense against predators can take the form of morphologic and behavioral adaptations. Any changes in the afarines' locomotor abilities were mostly behavioral. If it was necessary to move through a dangerous area it might best be done by small, quiet groups moving at night. On the

other hand, a large noisy group moving in the middle of the day may have been a successful alternative. There is a number of possible solutions and we do not know which one(s) the afarines adopted. It could have been several, but what ever course they adopted, it worked.

Not only must an organism be capable of moving safely, but also of making intelligent moves. I do not mean intelligent in the sense that the creature sat down and, in a logical, sequential manner, reasoned out the pros and cons of the situation. This would be a highly adaptive behavior, and it would be nice if we always behaved that way today. All that would be necessary though, is the ability to remember things seen or done previously (either last week or last year) and to be able to recognize a pattern in events and spatial relationships. An organism needs enough intelligence to organize its movements in relation to the distribution of its food sources in space and time. In an environment as subject to disturbance as the Rift Valley, a long-lived organism can benefit from the ability to remember events of the distant past (e. g. where water was found during the long drought all those years ago) (MacKinnon 1977; Moss 1988).

A mosaic habitat contains a variety of foods at any one time and also seasonally. These foods are useless if an organism does not or cannot eat them. Primates are, for the most part, omnivores (Butynski 1982; Rose 1978; Teleki

1975). They include both plant and animals in their diet. Some, like the leaf-eating colobines (Owen 1980; Washburn 1950), have, secondarily, adapted to a more limited diet. For a primate, like the australopithecines, many different foods can be eaten, it is just a question of learning and remembering what plants are edible. There are, of course, some foods that are edible only after using the teeth and jaws for preparation. There are also foods which put quite a bit of mechanical stress on the teeth and jaws during mastication. Both these factors would favor changes in the cranio-dental complex and/or in the use of tools to prepare the food.

Primates are social animals. Social organization is more than a means of regulating reproduction and the raising of infants, social organization is also a form of adaptation to the environment (Eisenberg, Muckenhirn, and Rudran 1972). A rigid, inflexible social organization can be adaptive, particularly in a stable environment. In an environment that can change quickly, radically and moreover, an environment which is diverse, the ability to alter one's social organization is more adaptive. A flexible social organization requires flexible behavior, which in turn requires some intelligence and an ability to learn and remember.

A general increase in intelligence is, usually, adaptive, definitely so in this instance of the australopithecines. It is also difficult to separate any selective

pressure for an increase in intelligence from an increase in intelligence caused by other adaptive trends. They all would benefit from an increase in the intelligence of the organism. (Intelligence in this case, could well be defined as "problem-solving ability.")

These adaptive trends would be expressed in the fossil record by changes in the skeleton. The most obvious of these would be changes in the foot, ankle, knee and hip which improve the bipedal capabilities of the organism, changes in the teeth, jaws, and skull that would improve the ability of the organism to eat the various foods, and an increase in cranial capacity to allow for an increase in the size of the brain and, therefore, a more intelligent organism. These changes would be based on the already existing skeleton, and compatible with it. There are some changes that would not be directly visible, if at all, in the fossil record. Changes in the social organization do not fossilize, although some aspects of social organization may be detectable in the fossil record (e. g. large canines for intraspecific dominance displays or a sexually dimorphic body size), but interpretation of the evidence can be difficult (large canines and large body size can be a defensive mechanism against predation).

The afarines seem to have been a moderately successful group. They survived, diversified and expanded their geographic range. As mentioned above, the afarines were al-

ready bipedal, although there are arguments about just how efficient, how completely bipedal they were (Jungers 1982; Langdon 1985; Lovejoy, Heiple, and Burstein 1973; McHenry and Temerin 1979; Stern and Susman 1983; Susman, Stern, and Jungers 1985; Wolpoff 1983). There was little selective pressure to alter that aspect of their morphology, the australopithecines were adequately adapted (physically) to bipedalism. It would be several million years, with the evolution of *Homo habilis*, before the brain began to expand rapidly and the hominid pelvis changed to allow the birth of large-brained infants. Bipedalism and the need to give birth to large-brained infants resulted in a conflict in the morphology of the pelvis, the "obstetrical dilemma." The female australopithecines may or may not have had some difficulty giving birth (Berge, Orban-Segebarth and Schmid 1984; Leutenegger 1972; Tague and Lovejoy 1986) but there was little selective pressure for changes in the morphology of the lower limbs. There have been claims that *A. afarensis* was arboreal, as indicated by their long arms, and therefore poorly adapted to bipedalism (Stern and Susman 1983; Susman, Stern, and Jungers 1985). I think that this misses one of the points about evolution: most changes occur because there is a selective advantage to be gained by the change. The long arms of the early australopithecines are from their primate, arboreal, heritage (McHenry 1978). The changes that occurred because of their adaptation to

bipedalism, occurred in the legs and pelvis. They were bipedal (Wolpoff 1983), although perhaps different from the bipedalism in *Homo sapiens* (Jungers 1982). The arms remained long, after the adoption of bipedalism, because there was either no selective pressure to reduce arm length, or long arms were still advantageous. The trees could provide some protection from some predators, and there was food to be gathered from the trees.

The afarine diet must have been broadly based (Blumenschine 1987; Dennell 1979; Dunbar 1976; Isaac 1971; Lucas, Corlett, and Luke 1985; Peters and Maguire 1981; Peters and O'Brien 1981; Speth 1987), and included a variety of vegetable foods (fruits, nuts, seeds, leaves, buds, roots, tubers and grass) and an assortment of animal foods (insects, grubs, reptiles, small mammals and carrion). They probably ate everything that would fit in their mouths and that did not actually poison them (Glander 1982). The afarines utilized whatever food was available, and were not dependent on any one particular food source. Around 3.0 M. Y. A., the descendants of these early australopithecines appeared in South Africa, and they had changed. These gracile australopithecines had larger bodies, their faces were less prognathic, and their brains were larger (part, or all, of the increase in brain size may have been allometric). As the original afarine populations adapted to the environment of eastern Africa their numbers would have

increased. Eventually the carrying capacity of the habitats would have been reached and population growth would have leveled off. A slightly larger population could be maintained if some populations of afarines specialized in more intensive exploitation of different portions of the habitat. Rather than using all of the various micro-habitats, more or less equally, one population might spend more time in the gallery forests along the rivers, learning to forage more intensively for food there. Another population might specialize in exploiting grassy savannahs, and a third populations might specialize in exploiting the bushy areas. This is not to say that they did not use the other habitat areas. They did, just not to the same extent as other populations did, spending more time in their particular favorite micro-habitat. While this specialization could allow for an increase in population numbers and, as I will demonstrate below, have some very important ramifications, there was another way of increasing population numbers: territorial expansion.

For a species like the afarines, who were specializing in behavioral flexibility, expansion of their geographic range would not be particularly difficult, nor unexpected. As populations expanded, they would have spread much more rapidly in environments only slightly different from those to which they were already adapted, making slight changes to adjust to the new environment. Eventually, though, they

would reach an environment that was more than a little different from the original environment, which might be thousand of niches and thousands of years distant in space and time. This much different environment would exert different selective pressures on the population of organisms.

In South Africa, the gracile australopithecines had encountered an environment that had some fundamental similarities to the environment in eastern Africa; but there were also some important differences. The gracile australopithecines were larger than the afarines. Although there is a trend in mammalian evolution for an increase in body size over time, this particular case may be better explained by Bergman's Rule (Wallace 1979). Bergman has pointed out that in many mammalian species that have a geographically wide north-to-south distribution, the individuals in the more northerly latitudes are generally larger than those individuals in the more southerly latitudes. This increase in body size is an adaptation to the cooler average temperatures, and the colder winters of the northern latitudes. This applies to humans just as well as to other animals (Roberts 1952). Bergman's Rule is applicable to the southern hemisphere just as well as it is to the northern hemisphere. What is meant by north is closer to the pole, and south means closer to the equator. The gracile australopithecines were living in the temperate latitudes, the

summers were not quite as hot as the summers in eastern Africa. Although the winters in South Africa were, and are not winters in the sense of sub-zero temperatures snow and icy winds, they are seasons of temperatures lower than those temperatures that normally occur in the topics. The gracile australopithecines became larger as an adaptation to the cooler temperatures.

The vegetation in South Africa is bush and grassland, it does not have the diversity of habitats that the Rift Valley does, at least not the same mosaic pattern of micro-habitats. South Africa does have more than one habitat, the Transvaal has more than the bush-and-grassland habitat. The difference is that the bush-and-grassland habitat is the primary habitat, covering much of the area, and the others exist as "islands" within or bordering it. Also, South Africa is much more stable, geologically, than eastern Africa. Changes in vegetation are responses to long-term climatic changes. The adaptive response of one population in one area of South Africa would be very similar to the adaptive response of another population somewhere else in South Africa. It would not be likely that two populations living side-by-side would be adapting to two different niches in two different ways. This situation would be reflected in the fossil record by a decrease in morphologic variability, when the fossils from South Africa are compared to the fossils from eastern Africa. While the early fossils

from South Africa could be and are, quite different from the later South African fossils, they will not show as much morphologic diversity across the whole of South Africa, at the same time period, as one finds in eastern Africa within an equivalent area. All the australopithecines in South Africa were evolving in response to the same selective pressures. The biggest changes were adaptations to their diets.

About 2.5 M. Y. A. the climate in Africa became drier. This increased aridity was marked by a shift in vegetation in South Africa, bush was replaced by grass (Vrba 1985b). Plants and animals had been adapting, since at least the end of the Miocene, to the increasing aridity, and the change after 2.5 M. Y. A. only increased selective pressure to adapt to an arid environment. Plants adapt to arid conditions by a period of dormancy during the dry periods (which in South Africa occurs during the winter), and by storing nutrients underground in the roots or tubers, to protect the nutrients from the dryness (Coursey 1973; Hatley and Kappelman 1980; Owen 1980). There is some evidence to indicate that many plants with underground storage systems developed them during and after the Miocene (Hatley and Kappelman 1980). The result of this adaptive trend of plants, was an increase in the "woodiness" of vegetable foods, they became more fibrous. Plant forage required more chewing, it was more abrasive and, during the dormant season the above-ground parts were lower in nutritive value. More

foods, that already took longer to eat, had to be eaten. The effects of this can already be seen in the gracile australopithecines; it is the major difference between them and their descendants, the robust australopithecines.

The morphologic adaptations of the Plio-Pleistocene hominids that resulted from the changes in the vegetation, are an inter-related complex of traits concentrated in the cranium and dental apparatus (the cranio-dental complex). The gracile australopithecines show evidence of beginning to adapt to a rougher, coarser diet McHenry 1984; Peters and Maguire 1981; Robinson 1954b; Wolpoff 1973a, 1973b). Their molars were becoming larger, primarily in terms of area of the bite surfaces. This increased their ability to process large amounts of foods, and to process rough, fibrous foods. The reduction of facial prognathism is also an adaption to a rougher diet. It is no accident that the teeth used for the heavy chewing are located closest to both the pivot point of the jaw and under the muscles that move the jaw (Molnar and Ward 1977). This provides for greater mechanical efficiency and force during mastication. The reduction in facial prognathism was not a direct adaptation to heavier mastication but a side effect of the adaptation. As the jaw rotated under the skull to increase bite force, the anterior portion of the jaw shifted backward, closer to the facial plane. This also had the effect of reducing stress on the anterior teeth and maxilla (Rak 1985a).

The robust australopithecines continued and accentuated this adaptive trend (McHenry 1984; Wolpoff 1973a). South Africa was becoming progressively drier, and the australopithecines relied, increasingly, on rougher forage to survive the dry, winter season (du Brul 1977; Grine 1981, 1986; Puech and Albertini 1984; Puech, Albertini, and Serratrice 1983; Rak 1985b; Wallace 1973). Not only were the molars larger, but the premolars were also larger and becoming molariform. For a bipedal animal like the australopithecines, there was a limit to how far under the skull the jaws could rotate. Eventually, the jaws could not rotate any further backwards, the cervical vertebrae would interfere with the chewing and swallowing of food. The increasing size of the molars and the molarization of the premolars required a longer tooth row. This would partially negate the effects of rotating the jaw under the skull. The teeth were moving to a better position closer to the temporal-mandibular joint and the temporal and masseter muscles to improve their chewing abilities, at the same time as they were enlarging and requiring a longer mandible and maxilla, which could only become longer by increasing facial prognathism. That is, the face would become more prognathic, unless the anterior teeth were reduced in size, allowing the molars and premolars, relative to canines and incisors, to occupy a greater proportion of the jaw. The canines, which may never been the projecting canines of the other primates

(Kinzey 1971), were even becoming part of the functional chewing apparatus. The robust australopithecines were doing enough heavy chewing that the stresses placed on the anterior teeth, and the supporting portions of the mandible and maxilla, were becoming important. Part of the stress was alleviated by the reduction of the facial prognathism, the remaining stress led to reinforcement of the mandible and the maxilla. The mandible simply became larger and thicker. This increase in mandibular robustness was a result of both the mechanical stress on the anterior teeth and the stress on the posterior teeth. The maxilla was remodelled to accommodate the stress. The upper incisors became implanted more vertically, so that the stress forces were transmitted parallel to the line of greatest strength of the maxillary bone and the area where the canines were implanted was reinforced. These "anterior pillars" (Rak 1985a) eventually extended from the canine tooth sockets up past the nose, acting as buttresses to strengthen the maxilla.

The increased forces, related to the mastication of rough forage, were generated, not by the forage but by the muscles involved in mastication (particularly the temporal and masseter muscles). Basically, if the muscles had not become larger and stronger, there would have been little need for the remodelling of the jaws and skull. With the gracile australopithecines, the enlargement of the brain provided enough enlargement of the exterior surface of the

cranial vault for the attachment of larger temporal and masseter muscles. However, the rate of skull enlargement of the robust australopithecines had not kept pace with the rate of enlargement in size of the muscles; some other way of providing attachment for the temporal and masseter muscles was needed. One of the most obvious differences between the robust and the gracile australopithecines is the presence of a sagittal crest along the top of the robust cranium (Robinson 1958; Wolpoff 1974). Its similarity to the massive bony flanges of a male gorilla (*Pan gorilla*) has led many to think that the robust australopithecines were like the gorillas in other respects. I do not think that they were. The robust australopithecines were little more than gracile australopithecines with big (robust) skulls. In fact, the sagittal crest is not identical to the crest in gorillas, which is actually a temporal-nuchal crest (Robinson 1958). The two crests are an example of convergent evolution in response to an identical problem, that is: providing sufficient area for the attachment of the muscles needed for the mastication of large quantities of tough fibrous vegetation. Had the robust australopithecines been quadrupedal animals like the gorilla, the crests would have been temporal-nuchal crest rather than sagittal crests. Because the robust australopithecines were bipedal, the muscles used in mastication were oriented vertically rather than more horizontally, hence, as the muscle mass increased,

the area of attachment expanded toward the sagittal suture. Eventually, the muscles had become so large that they met along the suture, then the ready solution to providing more area of attachment was the formation of a crest, between the two opposing muscle groups.

Increased muscle strength means increasing muscle mass, not just a greater area of muscle attachment. The increasing mass of the temporal and, especially, the masseter muscle, led to the lateral flaring of the zygomatic arch (the cheek bone), increasing the bizygomatic width. This, combined with the further reduction of facial prognathism, and the development of the anterior facial pillars (Rak 1985a), gave the robust australopithecine face a "dished-in," flat appearance. The nose did not protrude the way it does in modern *Homo sapiens*.

The South African australopithecines were a successful lineage. They survived in South Africa for at least two million years, until the appearance of another hominid, a more intelligent, tool-using being.

CHAPTER EIGHT

THE ECOLOGICAL MODEL:

EASTERN AFRICA

> The first step toward understanding is to stop assuming that humans win out in evolution *because they are human* [author's emphasis].
>
> -Richard Foly (quoted in Johanson and Shreeve 1989:252)

The australopithecine population in eastern Africa faced a situation similar to that of the South African australopithecines. There was an important difference though: the mosaic pattern of micro-habitats. It was possible, in eastern Africa, for more than one population of australopithecines to exist, each adapting to more than one set of selective pressures.

During the Pliocene, much of the environment in eastern Africa was a bush-and-grassland like that of South Africa, and one population of australopithecines evolved adaptations similar to the robust australopithecines. These eastern African robust australopithecines appear in the fossil record 2.5 M. Y. A., about 0.5 million years before the South African robust forms appear (Leakey and Walker

1988; Walker, Leakey, Harris, and Brown 1986). It is possible, indeed probable, that it was in eastern Africa where the selection pressure for the robust adaptations was the greatest and where the robust australopithecines evolved earliest. The australopithecine populations of eastern Africa and South Africa did not exist in isolation from each other. There was genetic continuity between the eastern and South African populations, populations of australopithecines certainly lived in Botswana, Zambia, Zimbabwe and Mozambique, the region between eastern and Southern Africa. The adaptations spread by gene flow southward, through these intervening populations of australopithecines to the populations in South Africa.

There was a least one other population of australopithecines in eastern Africa. This population was living in a different set of habitats from those of the robust australopithecines, and their adaptive response was taking a different tack. The eastern African robusts were adapting to the bush-and-grassland and savannah habitats by making greater use of the rougher forage. This adaptation enabled them to survive the long dry season of eastern Africa just as the same adaptations enabled the South African robusts to survive the winter season in South Africa, and if one could successfully survive those, the rainy season and summer would be downright easy to survive. The adaptation was also an adaptation to a general habitat type that stretched from

the Sudan to the Cape of Good Hope, and along the southern edge of the Sahara to the Atlantic Ocean. Wherever there was enough surface water, the robust australopithecines could find enough vegetable food to eat. Initially, it was an effective adaptive response. The robust australopithecines were able to colonize large areas of the African continent and, for a primate at least, in fairly large numbers. Since the late Miocene, the pongids were being displaced by the cercopithecine monkeys (Andrews 1981), but here was one pongid that had successfully shifted its niche and was able to increase its numbers and expand its range in the face of competition, competition that had nearly eliminated all of the other pongids.

Along the rivers and lakes of the Rift Valley, another competitor was evolving, one who's adaptation, that given time to perfect, would offer it more opportunity than could any other adaptation. I need to digress for a moment here, before I discuss the evolution of the "habiline" hominids, to clear up any possible misunderstanding or possible apprehension. The population of australopithecines that is ancestral to man, did not survive, did not evolve intelligence and culture because that would ultimately be a "better" adaptation, or because it would lead to modern man, *Homo sapiens*. Evolution occurs because an adaptation is advantageous, as it is now, not because it will be advantageous at some time in the future. Richard Dawkins pointed

this out quite clearly when he stated:

> Evolution has no long-term goal. There is no long-distance target, no final perfection to serve as a criterion for selection, although human vanity cherishes the absurd notion that our species is the final goal of evolution. In real life the criterion for selection is always short-term, either simple survival or, more generally, reproductive success. If, after the aeons, what looks like progress towards some distant goal seems, with hindsight, to have been achieved, this is always an incidental consequence of many generations of short-term selection. The "watchmaker" that is cumulative natural selection is blind to the future and has no long-term goal (1987:50).

The habilines evolved and survived because their adaptive response enabled a population to continue to live and exploit a particular niche more effectively than any other population. That these adaptations would eventually enable this small population hominids to displace all the other hominid populations, expand throughout the entire world and grow to a population in excess of five billion, is irrelevant. They survived because it worked, then. The future may demonstrate that, in the long-run it did not work but that possible outcome is also irrelevant. The habilines did not evolve culture (perhaps the word "invent" is more accurate) because they wanted to, just as the robust australopithecines did not evolve big molars, small incisors, flat faces and sagittal crests because they wanted to adapt to the environment in that way.

In eastern Africa there was, at least, one population of australopithecines that did not adapt to the changes in the environment by developing the suite of morphologic

traits that comprise the adaptive response of the robust australopithecines. The population, perhaps we should call them the proto-habilines, East African graciles, or advanced afarines, retained the morphologically generalized australopithecine body. This population was able to survive along the lakes and rivers of the Rift Valley. Their fossils are found in the sediments of the lake margins as commonly as the robusts fossils are found. In fluvial deposits, the robust fossils are found three times more often than those of the habilines (Behrensmeyer 1975). The habilines used both the lake margins and the rivers (fluvial areas), possibly in equal proportion. It was the robust australopithecines that used the different areas unequally. The savannah was the source of most of their food, the lake margins and riverine forests were a supplemental source of food and a major source of water. The fossils of robust australopithecines occur more frequently in the fluvial deposits because they were more likely to go to a river than to a lake for water and shade. The rivers cut through the savannah, offering better access to it than lakes do.

Along the lake margins the habilines were able to survive without the adaptations that characterize the robust australopithecines. They could not compete with them in the savannah or the veldt, they could hold their own in the relatively richer habitats along the rivers and lakes. These habitats were not as severe, as harsh, as those oc-

cupied by the robust australopithecines. It was not necessary for the habilines to eat, to be so dependent upon, rough, fibrous vegetable foods for survival. Not only that, but other animals are more common, alive and dead, nearer to water, and in the thicker vegetation. Meat would provide an alternate source of food when vegetable foods where scarce.

All the australopithecines were relatively intelligent, compared to other mammals. Their brain size to body weight ratios was higher than that of any other apes (Leutenegger 1973; McHenry 1975). Part of their behavioral repertoire was the use of tools. A number of animals make occasional use of tools. One of Darwin's finches uses a cactus spine to pry insects out of the bark of trees, and chimpanzees (*Pan troglodytes*) are well known to manipulate objects and use them as tools (Goodall 1986; Lancaster 1968); there is no reason that the australopithecines did not do so, too. That the robust australopithecines never became very dependent upon tools, at least for food processing, is evident in their teeth and jaws. The robust's cranio-dental complex demonstrates that their teeth and jaws were their food processing tools. A digging stick, to grub out roots and tubers, may have been their farthest advance in tool technology.

The habilines, though, took a crucial step beyond the robust australopithecines. The use of tools became their means of adaptation; they came to rely more and more on

tools, which, unlike teeth and muscles, can be forgotten, or lost. The knowledge of tool-use and manufacture can be lost if a generation fails to learn it. Captive orang-utans (*Pongo pygmaeus*) use tools, rivaling the chimpanzees with their skill (Lethmate 1982). Tool-use among wild orang-utans has been very rarely observed (MacKinnon 1974). It is thought (Lethmate 1982) that the orang-utan's solitary life impedes the transmission of the knowledge of tool-use. In a sense, orang-utans have to "re-invent the wheel" every generation or so, because the knowledge of using tools in not reliably passed on.

It was only a question of time before one population had transmitted knowledge of tool-use from one generation to another often enough that the effects began to accumulate. They had knowledge of more than one tool, and they had begun to manufacture tools. In the early stages, the use and manufacture of tools was still not critical for their survival. The habilines could survive without them, but the tools made life easier, and tool-use did enable them to begin to expand their range into the drier bush and into the savannah, into the habitat of the robust australopithecines. Their numbers increased, and soon, there were too many habilines for them all to survive in the old habitat without tools; now they were dependent on tools. They needed tools to make up for what the teeth, jaws and muscles of the robust australopithecines did for them.

Determining when tools became an important part of the hominid adaption is difficult. The first tools were unmodified natural objects (stone or organic) that, even if found, would not be recognized as tools. The first manufactured tools were certainly made from organic materials that were very unlikely to survive to be recovered and recognized. The first recognizable evidence we have of tools are those made of stone. The appearance of stone tools, which is dated to more than 2.0 M. Y. A. (Oakley 1970; Toth and Shick 1986), is conventionally used to mark the time when hominids became dependent on tools, when culture became the means of adaptation. I agree with this.

Although stone tools are not the first tools or even the first manufactured tools, they mark an important shift in man's relation to his world. The materials to manufacture stone tools are not as readily available as are wood and bone so one must plan ahead. Even making the tool requires advance planning. The finished tool has to be visualized and the steps necessary to form that idea have to be arranged in sequence. The hominids began to very actively manipulate their environment. The increased ability to think, to solve problems became important, as did the ability to successfully pass the accumulated knowledge (to learn and remember) on to the next generation.

The habilines began to occupy more and more of the habitat of the robust australopithecines. The robust aus-

tralopithecines did not have quite the intellectual capability of the habilines or the accumulated knowledge to build upon. They had some morphologic adaptations that enabled them to compete for use of the more marginal habitats. In a sense though, this made the situation worse. In the short-term, becoming "hyper-robust" was competitive. The hyper-robust australopithecines could survive for a while longer by specializing in the exploitation of a part of the habitat that the habilines could not use as effectively. But, they were trapped in it. Physical evolution was slower than technological adaptation; it also led to increasing specialization. The changes in the squamosal suture of *Australopithecus boisei* are an example of this physical specialization. The increase strength of the muscles, increased the stress placed upon the bones and the sutures of the skull. The squamosal suture, in particular, would have to resist the greater pressure placed upon it during mastication. The squamosal suture of the robust australopithecines had altered to resist this increased stress (Rak 1978). The suture had a beveled edge that increased the contact surface between the temporal and the parietal bone, this increased the strength of the suture.

It was the competition between these two populations of hominids, that were originally identical, that led to a result different from what had happened in South Africa. The environment in eastern Africa, primarily the Rift Valley

area, had enough different niches available for several different populations of hominids to adapt to different ways of life (ecological separation). However, one population, the habilines, evolved a way of life that enabled it to expand and usurp the range, the niche, of the second population, the robusts. The robusts adjusted to this increasing competition by becoming more "robust," more highly adapted to their particular niche, they became "hyper-robust." But in the end it didn't work.

Physical evolution can proceed only as fast as genetics will permit. The hyper-robust australopithecines could not adapt fast enough to another habitat to occupy it before the habilines could. Eventually, when the habilines occupied all of the habitats, there was no place for them.

By then, the habilines had become something different. They were no longer australopithecines, they were early humans. As such, they spread rapidly throughout the Old World land mass, adapting readily to a very wide range of habitats. Many of the changes must have been in behavior, social organization and in knowledge, because the tools remain much the same throughout the Old World for hundreds of thousands of years. The brain became larger but the body did not change much.

In South Africa, the robust australopithecines did not survive long enough to develop the hyper-robustness that had developed in east African robust australopithecines. Adap-

tation by physical evolution could not, cannot, match the speed of cultural adaptation.

CHAPTER NINE

CONCLUSIONS

> Plausibility simply demonstrated that given a line of research is a rational endeavor. Research stemming from such arguments of plausibility ought to result, one hopes, in the production of reliable methods for inference.
>
> - L. R. Binford 1983:75

Plausibility alone is not the test of a model's accuracy. A model, or hypothesis, will require several conditions that must be met in order to demonstrate its validity. A good model will also predict some things that further work or testing will demonstrate. If these necessary conditions are not met and predictions are not found to be as predicted, the model, or hypothesis, is either wrong or needs to be altered. This is the scientific method. Bernard Campbell stated (1973) that science progresses by revising every hypothesis, each succeeding hypothesis a better approximation than the preceding hypothesis. Looking at it in another way:

> It follows that each worker must be prepared to change his mind. Because of the nature of scientific progress outlined above, it is clear that we are all wrong all of the time. Given this conclusion, it also follows that we must be prepared to move forward from one fallacy to another, given that the latter is somewhat less fallacious. The ability to change one's mind may be considered

> undesirable in some areas of man's endeavor, but is absolutely essential if science is to progress (Campbell 1973).

I do not think that my model is correct in all of its aspects, for that matter, I changed my own ideas on several points while writing this thesis, and I expect to have it demonstrated that I was wrong in at least a few points. I hope that it will be demonstrated that my model is a more nearly accurate explanation of what has been found than are other proposed models or explanations. This model is a bit sparse in specific details; it was meant to be so. It was meant to be a general model, the specific details can be added on later as they are worked out.

The proposed model predicts some aspects of the paleontological and archaeological record that are tests of a model's validity, of its plausibility. If the facts as now known, or as determined in the future, are contrary to what the model predicts, then the model is false and must be discarded. Other prediction, if demonstrated to be false, will require that the model be altered to accommodate the new facts to remain plausible.

If the afarine australopithecines are the stem hominid, then they will be the earliest known fossils, the ones with the earliest known time range. The afarines may not be the earliest of the australopithecines in South Africa, or anywhere else outside eastern Africa, however they will occur in eastern Africa earlier than they occur anywhere

else. Indeed the model predicts that the australopithecines that appear in South Africa will not be afarines; adapting to the changing environment, they will have evolved into another kind of australopithecine: the gracile australopithecine.

If the gracile australopithecines are the ancestors of the robust australopithecines, they will always be found in the older South African fossil deposits. The geologically younger gracile australopithecines will be (morphologically) more like the geologically oldest robust australopithecines than will the geologically older gracile australopithecines. If enough hominid fossils, of the right age, could be found in South Africa, the gracile and robust australopithecines would show a morphologic range that merges, with no separation between, the two types. One of Wolpoff's arguments (1973b) for there being only one australopithecine species was that the size ranges of their posterior teeth of the gracile and robust australopithecines overlapped. This is precisely the situation one would expect to find in the case of one population (or species) evolving (by anagenesis) into another population (or species).

The relationship between the South African robust australopithecines and the eastern African robust and hyperrobust australopithecines is complex. The "black skull", KNM-WT 17000 indicates that the complex of traits that represent the robust adaptive response, appears earlier in

eastern Africa than in South Africa. The complex of traits need not have arisen independently in eastern and southern Africa. The robust adaptation could appear first in eastern Africa and spread to the South African populations, which were adapting to a similar niche. This does not mean the gracile australopithecines were not the ancestors of the South African robusts. There was not a population of eastern African robust australopithecines migrating to South Africa (Dr. Thomas Foor's "burly gang" scenario, personal communication) and replacing the gracile population. It was the genetic coding for the robust adaptation that was passed from one population to another, where it was adaptive. With the appearance of the hyper-robust eastern African australopithecines there developed a morphologic cline between the hyper-robust australopithecines and the South African robust australopithecines.

It is major hypothesis of the ecological model that in eastern Africa two different adaptive responses occurred in the australopithecine populations because they were inhabiting several different habitats and adapting to more than one niche. The multiplicity of habitats in eastern Africa (the mosaic of micro-habitats) explains the morphologic variability seen in the australopithecine fossils found in eastern Africa. The morphologic variability is a response to the many possible niches to which australopithecine populations were adapting.

If the habilines evolved in a way different to that of the robust australopithecines, it was because they were living in a different habitat. Therefore, the fossils of the eastern African robusts and the habilines should be found in different sedimentary rocks that reflect this difference in habitat choice. This need not be a mutually exclusive distribution; both types of fossils can be found in the sedimentary rocks. However, one type will be more numerous in the strata of one habitat, than the other type of fossil, in other strata from other habitats the situation would be reversed.

I am not satisfied with the scenario I presented in model, that of the habilines occupying the margins of the lakes, and the robust australopithecines occupying the savannah. I proposed this division of niches and constructed what seems to be a plausible scenario of why this led to the evolution of *Homo*, because there is some evidence to support this habitat division (Behrensmeyer 1975). Further research is needed to determine if the difference in the distribution of the fossils is real rather than an artifact of preservation. A real difference in the distribution of fossils in relation to the environment of deposition indicates a real difference in the use of the environment; this is a clue to how the two hominid populations coexisted and eventually evolved in two different ways.

If the hyper-robust australopithecines were the result of an adaptive response to increasing competition with the habilines, then they will be found only in eastern Africa and, only from the strata of the same age as those containing the habilines and/or *Homo erectus*. In South Africa, the robust australopithecines did not have sufficient time to evolve the hyper-robust features that characterize the eastern African forms. Their extinction occurred before the process could proceed far enough. The last of the South Africa australopithecines should show a trend in the direction of hyper-robustness, perhaps that is what is being seen in the fossils that have be called *Australopithecus crassidens* (Broom 1949). The habilines themselves should only be found in eastern Africa. It may be possible that the later habilines had begun the geographic expansion that characterizes *Homo erectus*. In this case, the oldest habilines will be found in eastern Africa and any found elsewhere (for instance: South Africa), will be found in younger deposits.

Homo erectus, the later robust australopithecines in South Africa, and the hyper-robust australopithecines in eastern Africa, will overlap in time and space. I do not want to give the impression that the extinction of australopithecines was due to *Homo erectus* killing them. I believe that they peacefully coexisted. The problem was that *Homo erectus* was exploiting the environment more effectively than

the robust australopithecines, increasing in numbers, occupying more space and consuming a greater portion of the food resources. It became harder and harder for the australopithecines to obtain enough food to support a viable population. Their population numbers declined and eventually they disappeared altogether.

There have been claims of Asian australopithecines (Robinson 1953a, 1955, 1963b). There is no reason, *a priori*, that there could not be Asian australopithecines. As I have stated above, I believe that the fossils are of *Homo erectus*. Should fossil remains of australopithecines be found in Asia, my model will be able to accommodate their presence, even if the fossils are older than the ones found, so far, in Africa. The eastern African robusts were, for a while any how, a successful population of hominids, and it is not beyond the realm of possibility that their range expanded to include parts of Asia. There is an implicit assumption here that it is a population of robusts australopithecines that would have reached Asia, and not an earlier population of gracile australopithecines. Part of this is based on the fact that those Asian fossils that have been claimed to be australopithecines have been attributed to the robust australopithecines (Robinson 1955). Descendants of the gracile australopithecines did reach Asia, we call them *Homo erectus*. There are two reasons why the robust australopithecines might have reached Asia: population pressure

as their populations increased, or pressure exerted by *H. erectus*. If it was pressure of an expanding population of australopithecines that led to their reaching Asia, any fossils found in Asia would be closely related to the earlier eastern African australopithecines. If the Asian australopithecines were "driven" to Asia by competition from *H. erectus*, then any fossil found should be similar to the later hyper-robust australopithecines.

Until now, I have deliberately avoided the use taxonomic names (Simpson N_3 name) when referring to the australopithecines. I have done this for several reasons. The use of taxonomic names implies phylogenetic relationships with which the user of the name may or may not be in agreement. Also, giving a scientific name to a population implies a degree of "separateness" (genetic or morphologic) from other populations, and a degree of precision in defining the boundaries of the population. I wanted to avoid these potential problems, believing that the use of taxonomic names would unnecessarily "cloud the issue." I have seen several phylogenies that seem to be little more than a few taxonomic names connected by a pattern of lines. It is as if, by drawing a line connecting one name with another name, as opposed to a different name, is a sufficient explanation. Many of the arguments about australopithecine evolution appear to revolve around how to connect the names, without regard to the "how" or "why" such an event represented by

the line may have occurred. That is the intent behind the ecological model, to develop a foundation that begin to explain the "how" and "why", upon which a phylogeny can be constructed. It is not that I did not imply a phylogenetic relationship with the model. It is there, I just did not specify the level involved (subspecific, specific, or generic)..

The degree of morphologic variation among the australopithecines is sufficient to warrant the division of the australopithecines into two or more species. These species would not necessarily be species in the same sense that the term is used to when discussing contemporary species (incapable of fertile interbreeding). They would be paleospecies and defined on the basis of geography, time and morphology. I think the concept of "superspecies" is applicable to the australopithecines. As G. G. Simpson explained:

> A superspecies is a monophyletic group of very closely related and largely or entirely allopatric species.
>
> Superspecies are, in other words, groups of populations that seem on other grounds (morphology, ecology, etc.) to have passed beyond the point of potential interbreeding and to have acquired separate evolutionary roles but that are not demonstrated to have done so by the more conclusive evidence of remaining separate when sympatric. It is to be assumed that they are still near the critical point of speciation, that of definitive isolation, and it cannot be quite certain whether they are really past that point and are not just below it. They are nascent species, that will, if they survive, collectively form a subgenus or eventually a genus but have hardly yet reached that degree of divergence and expansion.

> They are not given special names; the rules of nomenclature make no provision for that. Usual designation is by the name of an included species as for species groups, some but not all of which are in fact superspecies *sensu* Mayr (1961:180-181).

Within this superspecies, which we can name *Australopithecus africanus*, after the first known specimen, I would include the following species: *A. africanus*, *A. afarensis*, *A. robustus*, *A. boisei*, and a yet unnamed species of eastern African graciles. Also included in this superspecies, although I will argue for a different genus name, is the closely related transitional species: *Homo habilis*.

J. T. Robinson argued that the robust australopithecines should be placed in a genus ("Paranthropus") different from the gracile australopithecines because the robusts represented a different adaptive trend. (Did I not promise that I would come back to this point?) Simpson pointed out:

> Different genetical species that back any determinable anatomical or ecological distinction are single species under the evolutionary definition: they do not have definably separate evolutionary roles" (1961:160).

Cartmill emphasized the point:

> Taxonomic boundaries must reflect more than mere phylogenetic affinity; they must also mark important adaptive shifts that underlie the evolutionary trends characteristic of a radiating higher taxon: (1974:442).

It is the robust forms though, that continue the adaptive trend of the australopithecines. They belong in the genus *Australopithecus*, and it is the habilines that have taken a different adaptive trend. The habilines are a

transitional species between the australopithecines and the pithecanthropines. As a group, the fossils usually considered to be *Homo habilis* are poorly defined (Tattersall 1986). It was remarked about one fossil (OH 62) attributed to *Homo habilis*, that is was an australopithecine from the neck down (Johanson, Masao, Eck, White, Walter, Kimbel, Asfaw, Manega, Ndessokia, and Suwa 1987). The habilines appear in the fossil record for a short period of time (possibly for only 300,000 years) and it can be difficult to decide if the fossils represent an australopithecine, a pithecanthropine, or a habiline. The habilines are an advanced australopithecine; they have not quite reached the stage of evolution represented by *Homo erectus*. The habilines may not have the large brains or the cultural developments of *Homo erectus*, but they are well along on path; they are the first representatives of man: *Homo habilis*.

It is a capital mistake to theorize before you have all the evidence. Insensibly one begins to twist facts to suit theories, instead of theories to suit facts.

-Sherlock Holmes

That, at least, is my opinion--I am aware that it is easy for an author to mistake himself for a majority.

-G. G. Simpson (1953:137)

APPENDIX I

SYNONYMS FOR PLIO-PLEISTOCENE HOMINID FOSSILS

"Australopithecus aethiopicus" - robust australopithecines from Omo, and KNM-ER 1470

"Australopithecus habilis" - *H. habilis*

"Australopithecus prometheus" - *A. africanus*

"Australopithecus walkeri"- KNM-WT 17000

"Homo aethiopicus" - robust australopithecines from Omo, and KNM-ER 1470

"Homo africanus" - *A. africanus* and *A. robustus*

"Homo antiquus" - gracile australopithecines from East Africa

"Homo ergaster" - KNM-ER 1470

"Homo kanamensis" - *Homo erectus* or *H. sapiens*

"Homo leakeyi" - *Homo erectus*

"Homo transvaalensis" - *A. africanus* and *A. robustus*

"Meganthropus africanus" - *A. africanus*

"Meganthropus paleojavanicus" - *Australopithecus* sp. or *Homo erectus*

"Paranthropus crassidens" - *A. robustus*

"Paranthropus paleojavanicus" - *A. robustus*

"Paranthropus robustus" - *A. robustus*

"Paraustralopithecus aethiopicus" - *A. robustus* or *A. boisei*

"Plesianthropus transvaalensis" - *Australopithecus africanus*

"Tchadanthropus uxoris" - *Australopithecus africanus* or *H. erectus*

"Telanthropus capensis" - *A. robustus* or *H. erectus*

"Zinjanthropus boisei" - *A. robustus*

APPENDIX II

MUSEUM ACCESSION NUMBER LETTER CODES

AL Afar Locality, Ethiopia
BEL Belohdelie, Middle Awash Valley, Ethiopia
B.M.N.H. British Museum of Natural History (London, England)
BOD Bodo, Middle Awash Valley, Ethiopia
D16 Sterkfontein Rubble Dump 16
KA Kromdraai A (Faunal Site)
KB Kromdraai B (Australopithecine Site)
KNM Kenya National Museum
- -BC Baringo (Chemeron)
- -BK Baringo (Kapthurin)
- -BL Baringo (Kapthurin)
- -BN Baringo (Ngorora)
- -CH Chemoigut/Chesowanja
- -ER East Rudolf
- -LT Lothagam
- -LU Lukeino
- -WT West Turkana

L Omo Tuff L?
LH Laetoli Hominid
MAK Maka, Middle Awash Valley, Ethiopia
MLD Makapansgat Limeworks Deposit
OH Olduvai Hominid
SE West Pit of the Sterkfontein Extension Locality
SK Swartkrans
SKa Swartkrans Assemblages from the Primary (formerly Pink) Breccia
SKb Swartkrans Assemblages from: 1) Secondary (formerly Brown) Breccia, and 2) Fills of Channels forming at a relatively late stage through both the Primary and Secondary Breccias
SKW Swartkrans (Channel Fill Deposit?)
STS Sterkfontein Type Site
Sts Sterkfontein Type Site
StW Sterkfontein, West Pit (or Watts' excavations?)
TM Transvaal Museum (early finds from Taung, Kromdraai (B?), and Sterkfontein

REFERENCES CITED

Altmann, Stuart
1974 Baboons, Space, Time, and Energy. American Zoologist 14:221-248.

Andrews, Peter
1981 Species Diversity and Diet in Monkeys and Apes During the Miocene. In Aspects of Human Evolution. C. B. Stringer (Ed.). Taylor and Francis, London. pp 25-61.

Andrews, Peter, and Lawrence Martin
1987 Cladistic Relationships of Extant and Fossil Hominids. Journal of Human Evolution 16:101-118.

Arambourg, C., and Y. Coppens
1968 Découverte D'un Australopithécien Nouveau Dans les Gisements de L'omo. South African Journal of Science 64:58.

Ardrey, Robert
1961 African Genesis. Dell Publishing, New York.

Bates, Marston
1960 Ecology and Evolution. In Evolution After Darwin. Sol Tax (Ed.). University of Chicago, Chicago. Vol. 1:547-568.

Behrensmeyer, Anna K.
1975 Taphonomy and Paleoecology in the Hominid Fossil Record. Yearbook of Physical Anthropology 19:36-50.

Bell, R. H. V.
1971 A Grazing Ecosystem in the Serengeti. Scientific American 225(1):86-93.

Berge, Christine, Rosine Orban-Segebarth, and Peter Schmid
1984 Obstetrical Interpretation of the Australopithecine Pelvic Cavity. Journal of Human Evolution 13:573-587.

Bielicki, Tadeusz
1966 On "Homo habilis." Current Anthropology 7(5):576-580.

Bilsborough, Alan
1971 Early Hominids and Artifacts in South Africa. Antiquity 45:210-213.

Binford, L. R.
1977 Olorgesailie Deserves More Than the Usual Book Review. Journal of Anthropological Research 33(4):493-502.
1981 Bones: Ancient Men and Modern Myth. Academic Press, New York.
1983 In Pursuit of the Past. Thames and Hudson, New York.
1984 Butchering, Sharing, and the Archaeological Record. Journal of Anthropological Archaeology 3:235-257.
1985 Human Ancestors: Changing view of Their Behavior. Journal of Anthropological Archaeology 4:292-327.

Bishop, W. W.
1963 The Later Tertiary and Pleistocene in Eastern Equatorial Africa. In African Ecology and Human Evolution. F. Clark Howell and François Bourlière (Eds.). Aldine, Chicago. pp 246-275.

Bishop, W. W., and M. H. L. Pickford
1975 Geology, Fauna, and Paleoenvironments of the Ngorora Formation, Kenya Rift Valley. Nature 254:185-192.

Blumenschine, Robert J.
1987 Characteristics of an Early Hominid Scavenging Niche. Current Anthropology 28:383-407.

Boaz, N. T.
1977 Paleoecology of Early Hominidae in Africa. Kroeber Anthropological Society Papers 50:37-62.

Boné, Edouard L., and Raymond A. Dart
1955 A Catalog of the Australopithecine Fossils Found at the Limeworks, Makapansgat. American Journal of Physical Anthropology 13:621-624.

Bonnefille, R.
1985 Evolution of the Continental Vegetation: The Palaeobotonical Record from East Africa. South African Journal of Science 81(5):267-270.

Brace, C. Loring
1972 Sexual Dimorphism in Human Evolution. Yearbook of Physical Anthropology 16:31-49.
1980 Reply to Washburn. American Anthropologist 82:394-395.

Brace, C. L., P. E. Mahler, and R. B. Rosen
1972 Tooth Measurements and the Rejection of the Taxon "Homo habilis." Yearbook of Physical Anthropology 16:50-68.

Brace, C. Loring, Harry Nelson, and Noel Korn
1971 Atlas of Fossil Man. Holt, Rinehard and Winston, Inc., New York.

Brain, C. K.
1981 The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago, Chicago.
1985 Cultural and Taphonomic Comparisons of Hominids From Swartkrans and Sterkfontein. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp 72-75.
1987 Some Adaptations for Survival by African Hominids during the Last Five Million Years. South African Journal of Science 83 (10):610-612.

Brock, A., P. L. McFadden, and T. C. Partridge
1977 Preliminary Palaeomagnetic Results From Makapansgat and Swartkrans. Nature 266:249-250.

Broom, R.
1936 A New Fossil Anthropoid Skull from South Africa. Nature 138:486-488.
1937 The Sterckfontein Ape. Nature 139-326.
1938 The Pleistocene Anthropoid Apes of South Africa. Nature 142:377-379.
1949 Another New Type of Fossil Ape-Man. Nature 163:57.
1950 The Genera and Species of the South African Fossil Ape-Men. American Journal of Physical Anthropology 8(1):1-13.

Broom, R., and J. T. Robinson
1950 Man Contemporaneous with the Swartkrans Ape-Man. American Journal of Physical Anthropology 8(2):151-155.

Brown, Frank, John Harris, Richard Leakey, and Alan Walker
1985 Early *Homo erectus* Skeleton From West Lake Turkana, Kenya. Nature 316:788-792.

Butynski, Thomas M.
1982 Vertebrate Predation by Primates: A Review of Hunting Patterns and Prey. Journal of Human Evolution 11:421-430.

Butzer, Karl W.
1971 Another Look at the Australopithecine Cave Breccias

of the Transvaal. American Anthropologist 73:1197-1201.

Butzer, Karl W., Neil B. Todd, Bennett Blumenberg, and Russell Tuttle.
1974 Recent Thinking on Human Evolution. Current Anthropology 15(4):367-426.

Cadman, Ann, and Richard J. Rayner
1989 Climactic Change and the Appearance of *Australopithecus africanus* in the Makapansgat Sediments. Journal of Human Evolution 18:107-113.

Campbell, Bernard
1966 Human Evolution, an Introduction to Man's Adaptations. Aldine, Chicago.
1973 A New Taxonomy of Fossil Man. Yearbook of Physical Anthropology 17:194-201.
1988 Humankind Emerging, 5th Edition. Scott, Foresman and Company. Glenview, Illinois.

Cartmill, Matt
1974 Rethinking Primate Origins. Science 184:436-443.

Cerling, T. E., R. L. Hay, and J. R. O'Neil
1977 Isotopic Evidence for Dramatic Climactic Changes in East Africa During the Pleistocene. Nature 267:137-138.

Chamberlain, A. T. and B. A. Wood
1987 Early Hominid Phylogeny. Journal of Human Evolution 16:119-133.

Clark, W. E. LeGros
1955 The Os Innominatum of the Recent Ponginae with Special Reference to that of the Australopithecinae. American Journal of Physical Anthropology 13:19-28.
1964 The Fossil Evidence for Human Evolution, 2nd Edition. University of Chicago, Chicago.

Clarke, Ronald J.
1985a *Australopithecus* and Early *Homo* in Southern Africa. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp. 171-177.
1985b Early Acheulean with *Homo habilis* at Sterkfontein. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 287-298.

Clarke, R. J., and F. Clark Howell
1972 Affinities of the Swartkrans 847 Hominid Cranium. American Journal of Physical Anthropology 37:319-336.

Cole, Lamont C.
1960 Competitive Exclusion. Science 132:348-349.

Cooke, H. B. S.
1963 Pleistocene Mammal Faunas of Africa, with Particular Reference to Southern Africa. In African Ecology and Human Evolution. F. Clark Howell and François Bourlière (Eds.). Aldine, Chicago. pp 65-116.

Coppens, Yves
1966 An Early Hominid from Chad. Current Anthropology 7(5):584-585.

Corruccini, R. S., and H. M. McHenry
1980 Cladometric Analysis of Pliocene Hominids. Journal of Human Evolution 9:209-221.

Coursey, D. G.
1973 Hominid Evolution and Hypogeous Plant Foods. Man 8:634-635.

Dart, Raymond A.
1925 *Australopithecus africanus*: The Man-ape of South Africa. Nature 115:195-199.
1926 Taungs and Its Significance. Nature 26:315-327.
1948a The Makapansgat Proto-Human Australopithecus Prometheus. American Journal of Physical Anthropology 6(3):259-283.
1948b The Adolescent Mandible of Australopithecus Prometheus. American Journal of Physical Anthropology 6(4):391-409.
1949 The Predatory Implement Technique of Australopithecus. American Journal of Physical Anthropology 7(1):1-38.
1953 The Predatory Transition from Ape to Man. International Anthropological and Linguistic Review 1:201-218.
1955 Australopithecus Prometheus and Telanthropus Capensis. American Journal of Physical Anthropology 13:67-96.
1956 The Myth of the Bone-accumulating Hyena. American Anthropologist 58:40-62.
1959a Further Light on Australopithecine Humeral and Femoral Weapons. American Journal of Physical Anthropology 17:87-93.
1959b The First Australopithecus Cranium from the Pink Breccia at Makapansgat. American Journal of Physical Anthropology 17:77-82.
1962a From Cannon-bone Scoops to Skull Bowls at Makapansgat. American Journal of Physical Anthropology 20:287-296.

Dart, Raymond A. (cont.)
1962b A Cleft Adult Mandible and the Nine Other Lower Jaw Fragments from Makapansgat. American Journal of Physical Anthropology 20:267-286.
1962c The Makapansgat Pink Breccia Australopithecine Skull. American Journal of Physical Anthropology 20:119-126.
1964 The Ecology of the South African Man-Apes. Yearbook of Physical Anthropology 12:26-47.
1971 On the Osteodontokeratic Culture of the Australopithecinae. Current Anthropology 12(2):233-236.

Dawkins, Richard
1987 The Blind Watchmaker. W. W. Norton & Company, New York.

Day, Michael H.
1986 Guide to Fossil Man. University of Chicago, Chicago.

Day, M. H., Mary D. Leakey, and Todd R. Olson
1980 On the Status of *Australopithecus afarensis*. Science 207:1102-1103.

Day, M. H., and R. E. F. Leakey
1973 New Evidence of the Genus *Homo* from East Rudolf, Kenya. I. American Journal of Physical Anthropology 39:341-354.
1974 New Evidence of the Genus *Homo* from East Rudolf, Kenya (III). American Journal of Physical Anthropology 41:367-380.

Day, M. H., R. E. F. Leakey, A. C. Walker, and B. A. Wood
1975 New Hominids From East Rudolf, Kenya, I. American Journal of Physical Anthropology 42:461-476.
1976 New Hominids from East Turkana, Kenya. American Journal of Physical Anthropology 45:369-436.

Deacon, H. J.
1983 Another Look at the Pleistocene Climates of South Africa. South African Journal of Science 79(8):325-328.

Delson, Eric
1977 Catarrhine Phylogeny and Classification: Principles, Methods and Comments. Journal of Human Evolution 6:433-459.

Dennell, R. W.
1979 Prehistoric Diet and Nutrition: Some Food for Thought. World Archaeology 11(2):121-135.

DeVore, Irven, and S. L. Washburn
1963 Baboon Ecology and Human Evolution. In African Ecology and Human Evolution. F. Clark Howell and François Bourlière (Eds.). Aldine, Chicago. pp 335-376.

du Brul, E. Lloyd
1977 Early Hominid Feeding Mechanisms. American Journal of Physical Anthropology 47:305-320.

Dunbar, R. I. M.
1976 Australopithecine Diet Based on a Baboon Analogy. Journal of Human Evolution 5:161-167.

Dunbar, R. I. M., and E. P. Dunbar
1974 Ecological Relations and Niche Separation Between Sympatric Terrestrial Primates in Ethiopia. Folia Primatologica 21:36-60.

Ebling, J.
1985 The Mythological Evolution of Nudity. Journal of Human Evolution 14:33-41.

Eckhardt, R. B.
1976 Observed and Expected Variation in Hominid Evolution. Journal of Human Evolution 5:467-475.

Eiseley, Loren.
1952 Fossil Man: a Personal Credo. American Journal of Physical Anthropology 10(1):1-6.
1957 The Immense Journey. A Vintage Book, New York.

Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran
1972 The Relation Between Ecology and Social Structure in Primates. Science 176:863-874.

Evans, E. M. Nesbit, Judith A. H. Van Couvering, and Peter Andrews
1981 Palaeoecology of Miocene Sites in Western Kenya. Journal of Human Evolution 10:99-116.

Ferguson, Walter W.
1983 An Alternative Interpretation of *Australopithecus afarensis* Fossil Material. Primates 24(3):397-409.
1989 A New Species of the Genus *Australopithecus* (Primates: Hominidae) from Plio/Pleistocene Deposits West of Lake Turkana in Kenya. Primates 30(2):223-232.

Fitch, F. J., and J. A. Miller
1976 Conventional Potassium-Argon and Argon-40/Argon-39 Dating of Volcanic Rocks from East Rudolf. In Earliest

Man and Environments in the Lake Rudolf Basin. Yves Coppen, F. Clark Howell, Glynn Ll. Isaac, and Richard E. F. Leakey (Eds.). University of Chicago, Chicago. pp 123-147.

Flint, R. F.
1959 Pleistocene CLimates in Eastern and Southern Africa. Bulletin of the Geological Society of America 70:343-374.

Glander, Kenneth E.
1982 The Impact of Plant Secondary Compounds on Primate Feeding Behavior. Yearbook of Physical Anthropology 25:1-18.

Goodall, Jane
1986 The Chimpanzees of Gombe. Belknap Press of Harvard University, Cambridge.

Grine, Frederick E.
1981 Trophic Differences Between 'Gracile' and 'Robust' Australopithecines: A Scanning Electron Microscope Analysis of Occlusal Events. South African Journal of Science 77(5):203-230.
1985 Australopithecine Evolution: The Deciduous Dental Evidence. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp.153-167.
1986 Dental Evidence for Dietary Differences in *Australopithecus* and *Paranthropus*: A Quantitative Analysis of Permanent Molar Microwear. Journal of Human Evolution 15:783-822.

Groves, Colin P., and Vratislau Mazák
1975 An Approach to the Taxonomy of the Hominidae: Gracile Villafranchian Hominids of Africa. Casopis Pro Mineralogii A Geologii 20(3):225-247.

Halfpenny, James C., Roy Douglas Ozanne, and Elizabeth Biesiot
1989 Winter: An Ecological Handbook. Johnson Publishing Company, Boulder, Colorado.

Hall, Roberta.
1977 Paleobiology and Systematics of Canids and Hominids. Journal of Human Evolution 6:519-531.

Hardin, Garrett
1960 The Competitive Exclusion Principle. Science 131:1292-1297.

Harris, John M.
1985 Age and Paleoecology of the Upper Laetolil Beds,

Laetoli, Tanzania. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp 76-81.

Hatley, Tom, and John Kappelman
1980 Bears, Pigs, and Plio-Pleistocene Hominids: A Case for the Exploitation of Belowground Food Resources. Human Ecology 8(4):371-387.

Hay, Richard L., and Mary D. Leakey
1982 The Fossil Footprints of Laetoli. Scientific American 246(2):50-57.

Hewes, Gordon W.
1961 Food Transport and the Origin of Hominid Bipedalism. American Anthropologist 63:687-710.

Hill, Andrew
1976 On Carnivore and Weathering Damage to Bone. Current Anthropology 17(2):335-336.
1987 Causes of Perceived Faunal Change in the Later Neogene of East Africa. Journal of Human Evolution 16:583-596.

Hinrichsen, Don
1978 How Old Are Our Ancestors. New Scientist 78:571.

Horowitz, A.
1975 Preliminary Palaeoenvironmental Implications of Pollen Analysis of Middle Breccia from Sterkfontein. Nature 258:417-418.

Howell, F. Clark
1955 The Age of the Australopithecines of Southern Africa. American Journal of Physical Anthropology 13:635-662.
1978 Hominidae. In Evolution of African Mammals. V. J. Maglio and H. B. S. Cooke (Eds.). Harvard University, Cambridge. pp 154-248.

Hsü, Kenneth J., Lucien Montadert, Daniel Bernoulli, Maria Bianca Cita, Albert Erickson, Robert E. Garrison, Robert B. Kidd, Frederic Mèlierés, Carla Müller, and Ramil Wright.
1977 History of the Mediterranean Salinity Crisis. Nature 267:399-403.

Hughes, Alun R.
1954 Hyaenas Versus Australopithecines as Agents of Bone Accumulation. American Journal of Physical Anthropology 12:467-486.

Hughes, Alun R., and Phillips V. Tobias
1977 A fossil Skull Probably of the Genus *Homo* from Sterkfontein, Transvaal. Nature 265:310-312.

Isaac, Glynn Ll.
1971 The Diet of Early Man: Aspects of Archaeological Evidence from Lower and Middle Pleistocene Sites in Africa. World Archaeology 2(3):278-298.
1977 Olorgesailie: Archeological Studies of a Middle Pleistocene Lake Basin in Kenya. University of Chicago, Chicago.
1978a Food Sharing and Human Evolution: Archaeological Evidence from the Plio-Pleistocene of East Africa. Journal of Anthropological Research 34(3):311-325.
1978b The Food-sharing Behavior of Protohuman Hominids. Scientific American 238(4):90-108.

Jacob, Teuku
1972 The Absolute Date of the Djetis Beds at Modjokerto. Antiquity 46:148.

Johanson, Donald C., Fidelis Masao, Gerald G. Eck, Tim D. White, Robert C. Walter, William H. Kimbel, Berhane Asfaw, Paul Manega, Prosper Ndessokia, and Gen Suwa.
1987 New Partial Skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. Nature 327:205-209.

Johanson, Donald C., and James Shreeve
1989 Lucy's Child: Discovery of a Human Ancestor. Morrow, New York.

Johanson, Donald C., and Tim D. White
1979 A Systematic Assessment of Early African Hominids. Science 203:321-330.
1980 On the Status of *Australopithecus afarensis*. Science 207:1104-1105.

Johanson, Donald C., Tim D. White and Yves Coppens
1978 A New Species of the Genus *Australopithecus* (Primates: Hominidae) from the Pliocene of Eastern Africa. Kirtlandia 28:1-14.

Jungers, William L.
1982 Lucy's Limbs: Skeletal Allometry and Locomotion in *Australopithecus afarensis*. Nature 297:676-678.

Kalb, Jon E., Clifford J. Jolly, Elizabeth B. Oswald, and Paul F. Whitehead
1984 Early Hominid Habitation in Ethiopia. American Scientist 72:168-178.

Keith, Arthur
1947 Australopithecinæ or Dartian. Nature 159:377.

Kinzey, Warren G.
1971 Evolution of the Human Canine Tooth. American Anthropologist 73:680-694.

Lancaster, Jane B.
1968 On the Evolution of Tool-using Behavior. American Anthropologist 70:56-66.

Langdon, John H.
1985 Fossils and the Origin of Bipedalism. Journal of Human Evolution 14:615-635.

Laporte, Léo F., and Adrienne L. Zihlman
1983 Plates, Climate and Hominoid Evolution. South African Journal of Science 79(3):96-110.

Leakey, L. S. B.
1960 Finding the World's Earliest Man. National Geographic 118:420-435.
1963 Very Early East African Hominidae and Their Ecological Setting. In African Ecology and Human Evolution. F. Clark Howell and François Bourlière (Eds.). Aldine, Chicago. pp 448-457.
1966 *Homo habilis*, *Homo erectus* and the Australopithecines. Nature 209:1279-1281.
1973 Was *Homo erectus* Responsible for the Hand-axe Culture? Journal of Human Evolution 2:493-498.

Leakey, L. S. B., P. V. Tobias, and J. R. Napier
1964 A New Species of the Genus *Homo* from Olduvai Gorge. Nature 202:7-9.

Leakey, M. D., R. J. Clarke, and L. S. B. Leakey
1971 New Hominid Skull from Bed I, Olduvai Gorge, Tanzania. Nature 232:308-312.

Leakey, M. D., and R. L. Hay
1979 Pliocene Footprints in the Laetolil Beds at Laetoli, Northern Tanzania. Nature 278:317-323.

Leakey, R. E. F.
1972 Further Evidence of Lower Pleistocene Hominids from East Rudolf, North Kenya, 1971. Nature 237:264-269.
1973 Evidence for an Advanced Plio-Pleistocene Hominid from East Rudolf, Kenya. Nature 242:447-450.

Leakey, R. E. F., J. M. Mungai, and A. C. Walker
1971 New Australopithecines from East Rudolf, Kenya. American Journal of Physical Anthropology 35:175-186.

Leakey, R. E. F., and A. C. Walker
1973 New Australopithecines from East Rudolf, Kenya (III). American Journal of Physical Anthropology 39:205-222.
1976 *Australopithecus*, *Homo erectus* and the Single Species Hypothesis. Nature 261:572-574.
1980 On the Status of *Australopithecus afarensis*. Science 207:1103.
1985 Further Hominids from the Plio-Pleistocene of Koobi Fora, Kenya. American Journal of Physical Anthropology 67:135-163.
1988 New *Australopithecus boisei* Specimens from East and West Lake Turkana, Kenya. American Journal of Physical Anthropology 76:1-24.

Leakey, R. E. F., and B. A. Wood
1973 New Evidence of the Genus *Homo* from East Rudolf, Kenya. II. American Journal of Physical Anthropology 39:355-368.
1974 New Evidence of the Genus *Homo* from East Rudolf, Kenya (IV). American Journal of Physical Anthropology 41:237-244.

Lethmate, Jürgen
1982 Tool-using Skills of Orang-utans. Journal of Human Evolution 11:49-64.

Leutenegger, W.
1972 Newborn Size and Pelvic Dimensions of *Australopithecus*. Nature 240:568-569.
1973 Encephalization in Australopithecines: A New Estimate. Folia Primatologica 19:9-17.

Lewin, Roger
1985 Surprise Findings in the Taung Child's Face. Science 228:42-44.

Lovejoy, C. Owen, Kingsbury G. Heiple, and Albert H. Burstein
1973 The Gait of *Australopithecus*. American Journal of Physical Anthropology 38:757-780.

Lucas, P. W., R. T. Corlett, and D. A. Luke
1985 Plio-Pleistocene Hominid Diets: An Approach Combining Masticatory and Ecological Analysis. Journal of Human Evolution 14:187-202.

MacKinnon, John
1974 The Behavior and Ecology of Wild Orang-utans (*Pongo pygmaeus*). Animal Behavior 22:3-74.
1977 A Comparative Ecology of Asian Apes. Primates 18(4):747-772.

Maguire, Judy M.
1985 Recent Geological, Stratigraphic and Palaeontological Studies at Makapansgat Limeworks. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 151-164.

Maier, W.
1977 Chronology and Biology of the South African Australopithecines. Journal of Human Evolution 6:89-93.

Malone, David
1987 Mechanisms of Hominoid Dispersal in the Miocene East Africa. Journal of Human Evolution 16:469-481.

Mayr, Ernst
1950 Taxonomic Categories in Fossil Hominids. Cold Spring Harbor Symposium on Quantitative Biology 15:109-117.
1963 The Taxonomic Evaluation of Fossil Hominids. In Classification and Human Evolution. Sherwood L. Washburn (Ed.). Aldine, Chicago. pp 332-345.

McBroom, Patricia
1968 The Scarred Species. Science News 94:523-525.

McHenry, Henry M.
1975 Fossil Hominid Body Weight and Brain Size. Nature 254:686-688.
1978 Fore- and Hindlimb Proportions in Plio-Pleistocene Hominids. American Journal of Physical Anthropology 49:15-22.
1984 Relative Cheek-tooth Size in *Australopithecus*. American Journal of Physical Anthropology 64:297-306.

McHenry, Henry M., and L. Alis Temerin
1979 The Evolution of Hominid Bipedalism: Evidence from the Fossil Record. Yearbook of Physical Anthropology 22:105-131.

Molnar, Stephen, and Steven C. Ward
1977 On the Hominid Masticatory Complex: Biomechanical and Evolutionary Perspectives. Journal of Human Evolution 6:557-568.

Moss, Cynthia
1988 Elephant Memories: Thirteen Years in the Life of an Elephant Family. Fawcett Columbine, New York.

Napier, J. R.
1964 The Evolution of Bipedal Walking in the Hominids. Archives de Biologie (Liège) 75:Supplement, 673-708.

Oakley, Kenneth P.
1954 Dating of the Australopithecinae of Africa. American Journal of Physical Anthropology 12(1):9-27.
1970 Pliocene Men. Antiquity 44:307-308.

Odum, Eugene P.
1963 Ecology. Holt, Rinehard and Winston, Inc. New York.

Olson, Todd R.
1978 Hominid Phylogenetics and the Existence of *Homo* in Member I of the Swartkrans Formation, South Africa. Journal of Human Evolution 7:159-178.
1981 Basicranial Morphology of the Extant Hominids and Pliocene Hominids: The New Material from the Hadar Formation, Ethiopia, and Its Significance in Early Human Evolution and Taxonomy. In Aspects of Human Evolution. C. B. Stringer (Ed.). Taylor and Francis, London. pp.99-128.
1985 Cranial Morphology and Systematics of the Hadar Formation Hominids and *"Australopithecus" africanus*. In Ancestors: The Hard Evidence. Eric Delson (Ed). Alan R. Liss, New York. pp. 102-119.

Osborn, Henry Fairfield
1929 Is the Ape-Man a Myth? Human Biology 1:4-9.

Owen, Jennifer
1980 Feeding Strategy. University of Chicago, Chicago.

Partridge, T.C.
1985a Spring Flow and Tufa Accretion at Taung. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 171-187.
1985b The Palaeoclimatic Significance of Cainozoic Terrestrial Stratigraphy and Tectonic Evidence from Southern Africa: A Review. South African Journal of Science 81(5):245-247.

Peters, Charles R.
1979 Toward an Ecological Model of African Plio-Pleistocene Hominid Adaptations. American Anthropologist 81:261-278.

Peters, Charles R., and Brian Maguire
1981 Wild Plant Foods of the Makapansgat Area: A Modern Ecosystems Analogue for *Australopithecus africanus* Adaptations. Journal of Human Evolution 10:565-583.

Peters, Charles R., and Eileen M. O'Brien
1981 The Early Hominid Plant-Food Niche: Insights From an Analysis of Plant Exploitation by *Homo*, *Pan*, and

Papio in Eastern and Southern Africa. Current Anthropology 22(3):257-268.

Pfeiffer, John E.
1969 The Emergence of Man, 2nd Edition. Harper & Row Publishers, New York.

Pickford, M., D. C. Johanson, C. O. Lovejoy, T. D. White, and J. L. Aronson
1983 A Hominoid Humeral Fragment from the Pliocene of Kenya. American Journal of Physical Anthropology 60:337-346.

Pilbeam, David
1972a The Ascent of Man, An Introduction to Human Evolution. The MacMillan Company, New York.
1972b Adaptive Response of Hominids to their Environment as Ascertained by Fossil Evidence. Social Biology 19(2):115-127.

Pilbeam, D. R., and M. Zwell
1972 The Single Species Hypothesis, Sexual Dimorphism, and Variability in Early Hominids. Yearbook of Physical Anthropology 16:69-79.

Poirier, Frank E.
1973 Fossil Man, An Evolutionary Journey. The C. V. Mosby Company, Saint Louis.

Pope, G. G., and J. E. Cronin
1984 The Asian Hominidae. Journal of Human Evolution 13:377-396.

Potts, Richard
1984 Home Bases and Early Hominids. American Scientist 72:338-347.
1986 Temporal Span of Bone Accumulations at Olduvai Gorge and Implications for Early Hominid Foraging Behavior. Paleobiology 12(1):25-31.

Puech, Pierre-François, and Henri Albertini
1984 Dental Microwear and Mechanisms in Early Hominids from Laetoli and Hadar. American Journal of Physical Anthropology 65:87-91.

Puech, Pierre-François, Henri Albertini, and Claudia Serratrice
1983 Tooth Microwear and Dietary Patterns in Early Hominids from Laetoli, Hadar and Olduvai. Journal of Human Evolution 12:721-729.

Rak, Yoel
1978 The Functional Significance of the Squamosal Suture in *Australopithecus boisei*. American Journal of Physical Anthropology 49:71-78.
1985a Australopithecine Taxonomy and Phylogeny in the Light of Facial Morphology American Journal of Physical Anthropology 66:281-287.
1985b Systematic and Functional Implications of the Facial Morphology of *Australopithecus* and Early *Homo*. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp 168-170.

Read-Martin, Catherine E., and Dwight W. Read
1976 More on Faunal Analysis. Current Anthropology 17(3):531-533.

Rightmire, G. P.
1979 Cranial Remains of *Homo erectus* from Beds II and IV, Olduvai Gorge, Tanzania. American Journal of Physical Anthropology 51:99-116.

Roberts, D. F.
1952 Body Weight, Race and Climate. American Journal of Physical Anthropology 11:533-558.

Robinson, J. T.
1953a Meganthropus, Australopithecus and Hominids. American Journal of Physical Anthropology 11(1):1-38.
1953b Telanthropus and Its Phylogenetic Significance. American Journal of Physical Anthropology 11(4):445-501.
1954a The Genera and Species of the Australopithecinae. American Journal of Physical Anthropology 12(2):181-200.
1954b Prehominid Dentition and Hominid Evolution. Evolution 8:324-334.
1955 Further Remarks on the Relationship between "Meganthropus" and Australopithecus. American Journal of Physical Anthropology 13:429-445.
1958 Cranial Cresting Patterns and Their Significance in the Hominoidea. American Journal of Physical Anthropology 16:397-428.
1961 The Australopithecines and Their Bearing on the Evolution of Man and of Stone Tool-making. South African Journal of Science 57:3-13.
1963a Australopithecines, Culture and Phylogeny. American Journal of Physical Anthropology 21:595-605.
1963b Adaptive Radiation in the Australopithecines and the Origin of Man. In African Ecology and Human Evolution. F. Clark Howell and François Bourlière (Eds.). Aldine, Chicago. pp. 385-416
1965 *Homo 'habilis'* and the Australopithecines. Nature

205:121-124.
1972 The Bearing of East Rudolf Fossils on Early Hominid Systematics. Nature 240:239-240.

Rose, M. D.
1978 The Roots of Primate Predatory Behavior. Journal of Human Evolution 7:179-189.

Shipman, Pat, and Jane E. Phillips
1976 On Scavenging by Hominids and Other Carnivores. Current Anthropology 17(1):170-172.

Shipman, Pat, and Jane Phillips-Conroy
1977 Hominid Tool-making Versus Carnivore Scavenging. American Journal of Physical Anthropology 46:77-86.

Sigmon, B. A.
1977 Contributions from Southern and Eastern Africa to the Study of Early Hominid Evolution. Journal of Human Evolution 6:245-257.

Simons, E. L.
1967 The Significance of Primate Paleontology for Anthropological Studies. American Journal of Physical Anthropology 27:307-332.
1968 A Source for Dental Comparison of Ramapithecus with Australopithecus and Homo. South African Journal of Science 64(2):92-112.

Simons, Elwyn L., David Pilbeam, and Peter C. Ettel
1969 Controversial Taxonomy of Fossil Hominids. Science 166:258-259.

Simpson, George Gaylord
1950 Some Principles of Historical Biology Bearing on Human Origins. Cold Spring Harbor Symposium on Quantitative Biology 15:55-66.
1953 The Major Features of Evolution. Simon and Schuster, New York.
1961 Principles of Animal Taxonomy. Columbia University Press.
1963 The Meaning of Taxonomic Statements. In Classifications and Human Evolution. S. L. Washburn (Ed.). Aldine, Chicago. pp. 1-31.

Speth, J. D.
1987 Early Hominid Subsistence Strategies in Seasonal Habitats. Journal of Archaeological Science 14:13-29.

Stauffer, Robert C.
1957 Haeckel, Darwin and Ecology. The Quarterly Review of Biology 32(1):138-144.

Stern, Jack T. Jr., and Randall L. Susman
1983 The Locomotor Anatomy of *Australopithecus afarensis*. American Journal of Physical Anthropology 60:279-317.

Susman, Randall L., Jack T. Stern, Jr., and William L. Jungers
1985 Locomotor Adaptations in the Hadar Hominids. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp 184-192.

Sutcliffe, Antony J.
1970 Spotted Hyaena: Crusher, Gnawer, Digester and Collector of Bones. Nature 227:1110-1113.

Tague, Robert G., and C. Owen Lovejoy
1986 The Obstetric Pelvis of A. L. 288-1 (Lucy). Journal of Human Evolution 15:237-255.

Tattersall, Ian
1986 Species Recognition in Human Paleontology. Journal of Human Evolution 15:165-175.

Tattersall, Ian, Eric Delson, and John van Couvering
1988 Australopithecus. Encyclopedia of Human Evolution and Prehistory: Garland Publishing, New York. pp. 67-85.

Teleki, Geza
1975 Primate Subsistence Patterns: Collector-Predators and Gatherer-Hunters. Journal of Human Evolution 4:125-184.

Thompson, Philip
1975 A Cross-species Analysis of Carnivore, Primate, and Hominid Behavior. Journal of Human Evolution 4:113-124.
1976 A Behavior Model for *Australopithecus africanus*. Journal of Human Evolution 5:547-558.

Tobias, P. V.
1980 "*Australopithecus afarensis*" and *A. africanus*: Critique and an Alternative Hypothesis. Palaeontologia Africana 23:1-17.
1985a The Former Taung Cave System in the Light of Contemporary Reports and its Bearing on the Skull's Provenance: Early Deterrents to the Acceptance of *Australopithecus*. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 25-40.
1985b Ten Climacteric Events in Hominid Evolution. South African Journal of Science 81(5):271-272.

Toth, Nicholas, and Kathy D. Shick
1986 The First Million Years: The Archaeology of Protohuman Culture. In Advances in Archaeological Method and Theory. Michael D. Schiffer (Ed.). Academic Press, Orlando, Florida. pp 1-97.

Turner, A.
1986 Correlation and Causation in Some Carnivore and Hominid Evolutionary Events. South African Journal of Science 82(2):75-76.

Vogel, John C.
1985 Further Attempts at Dating the Taung Tufas. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 189-194.

Vrba, Elisabeth S.
1974 Chronological and Ecological Implications of the Fossil Bovidae at the Sterkfontein Australopithecine Site. Nature 250:19-23
1975 Some Evidence of Chronology and Palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the Fossil Bovidae. Nature 254:301-304.
1985a Ecological and Adaptive Changes Associated with Early Hominid Evolution. In Ancestors: The Hard Evidence. Eric Delson (Ed.). Alan R. Liss, New York. pp 63-71.
1985b Early Hominids in Southern Africa: Updated Observations on Chronological and Ecological Background. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 195-200.

Walker, A.
1976 Remains Attributable to *Australopithecus* in the East Rudolf Succession. In Earliest Man and Environments in the Lake Rudolf Basin. Yves Coppen, F. Clark Howell, Glynn Ll. Isaac, and Richard E. F. Leakey (Eds.). University of Chicago, Chicago. pp 484-489.

Walker, A., R. E. Leakey, J. M. Harris, and F. H. Brown
1986 2.5-MYR *Australopithecus boisei* from West of Lake Turkana, Kenya. Nature 322:517-522.

Wallace, J. A.
1973 Tooth Chipping in the Australopithecines. Nature 244:117-118.

Wallace, Robert A.
1979 The Ecology and Evolution of Animal Behavior. Goodyear Publishing Company, Inc. Santa Monica, California.

Walter, Robert C., and James L. Aronson
1982 Revisions of K/Ar Ages for the Hadar Hominid Site, Ethiopia. Nature 296:122-127.

Washburn, S. L.
1950 The Analysis of Primate Evolution with Particular Reference to the Origin of Man. Cold Spring Harbor Symposium on Quantitative Biology 15:67-78.
1960 Tools and Human Evolution. Scientific American 203(3):62-75.

Webster's II New Riverside University Dictionary
1984 Houghton Mifflin Company, Boston.

Wells, Calvin
1965 Bones, Bodies and Disease: Evidence for Disease and Abnormality in Early Man. Frederick A. Praeger, New York.

Wheeler, P. E.
1984 The Evolution of Bipedality and the Loss of Functional Body Hair in Hominids. Journal of Human Evolution 13:91-98.

White, Tim D.
1976 New Fossil Hominids from Laetoli, Tanzania. American Journal of Physical Anthropology 46:197-230.
1980 Additional Fossil Hominids from Laetoli, Tanzania: 1976-1979 Specimens. American Journal of Physical Anthropology 53:487-504.

Williamson, P. G.
1985 Evidence for an Early Plio-Pleistocene Rainforest Expansion in East Africa. Nature 315:487-489.

Winterhalder, Bruce
1980 Hominid Paleoecology: The Competitive Exclusion Principle and Determinants of Niche Relationships. Yearbook of Physical Anthropology 23:43-60.
1981 Hominid Paleoecology and Competitive Exclusion: Limits to Similarity, Niche Differentiation, and the Effects of Cultural Behavior. Yearbook of Physical Anthropology 24:101-121.

Wolfe, Kenneth Adelbert
1971 On the Possibility of Coexistence in Early Man. California Anthropologist 1(1):37-42.

Wolpoff, Milford H.
1968 "Telanthropus" and the Single Species Hypothesis. American Anthropologist 70:477-491.
1970 The Evidence for Multiple Hominid Taxa at Swart-

krans. American Anthropologist 72:576-607.
1971 Competitive Exclusion among Lower Pleistocene Hominids: The Single Species Hypothesis. Man 6(4):601-614.
1973a Posterior Tooth Size, Body Size, and Diet in South African Gracile Australopithecines. American Journal of Physical Anthropology 39:375-394.
1973b The Evidence for Two Australopithecine Lineages in South Africa. Yearbook of Physical Anthropology 17: 113-139.
1974 Sagittal Cresting in the South African Australopithecines. American Journal of Physical Anthropology 40:397-408.
1976a Primate Models For Australopithecine Sexual Dimorphism. American Journal of Physical Anthropology 45:497-519.
1976b Some Aspects of the Evolution of Early Hominid Sexual Dimorphism. Current Anthropology 17(4):579-606.
1983 Lucy's Little Legs. Journal of Human Evolution 12:443-453.

Wood, Bernard
1985 A Review of the Definition Distribution and Relationships of *Australopithecus africanus*. In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp.227-232.

Wood, B. A., and A. T. Chamberlain
1987 The Nature and Affinities of the "Robust" Australopithecines: A Review. Journal of Human Evolution 16:625-641.

Wood-Jones, F.
1947 The *Plesianthropus* Skull. Nature 159:883.

Yemane, Kedamawit, Raymonde Bonnefille, and Hugues Faure
1985 Palaeoclimatic and Tectonic Implications of Neogene Microflora from the Northwestern Ethiopian Highlands. Nature 318:653-656.

Zhilman, Adrienne L.
1985 Australopithecus afarensis: Two Sexes or Two Species? In Hominid Evolution: Past, Present and Future. P. V. Tobias (Ed.). Alan R. Liss, New York. pp 213-220.

Zhilman, A. L., and B. A. Cohn
1988 The Adaptive Response of Human Skin to the Savanna. Human Evolution 3(5):397-409.