To the Graduate Council:

I am submitting herewith a thesis written by Clare K. Stott entitled "Aspects of Ecology and Adaptation with an Emphasis on Hominoid Evolution". I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Anthropology.

Dr. Andrew Kramer, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School.

Aspects of Ecology and Adaptation with an Emphasis on Hominoid Evolution

A Thesis
Presented for the
Master of Arts
Degree
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Clare Katharine Stott
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In dedication
to my friend, my father
without whose continued love and support
I never could have come this far,

and

to my mother who,
in life and memory, has given me
the strength to strive and
succeed.

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Abstract

This thesis will explore hominoid evolution from the joint perspectives of ecology and palaeoanthropology. Unique to this study is the idea of Ecosystematics. While ecologists tend to focus their attentions on the immediate context of organismal existence and survival (i.e., the ecosystem), palaeoanthropologists more often focus on the long term, evolutionary trends of organismal adaptation, with usually much less attention given to the context of such adaptations. The Ecosystematic cycle bridges together these ideas of proximate (immediate context) and ultimate (long term) adaptation towards the end of better understanding of evolutionary patterns and processes inherent to hominid development. In this study, the key tenets, ideas and principles of both ecology and palaeoanthropology will be introduced and explored from the specific vantage of Miocene hominoid origins, proximate survival, immediate and long term adaptations and ultimate evolution. Ecological variables of climatic change, resource availability, kinds and degrees of competition, and geographic variability will all be explored. All such variables have repeatedly been shown to have greatly moderated the means and modes by which hominoids have adapted in response to and evolved in conjunction with an ever-changing suite of ecological circumstances. Definite trends in ecological variability as relating to hominoid evolution will be discussed. Such trends are of such a recurrent/predictable nature that they provide a great resource/knowledge base. It is through the direct access of such a knowledge base that palaeoanthropologists will be more readily able to interpret and understand the patterns and processes behind hominoid adaptation and evolution. In devising a more multi-dimensional, multi-disciplinary approach (i.e., Ecosystematics) the rhymes and reasons behind hominoid origins and evolution, both in ecological space and over evolutionary time, will be more clearly viewed and understood.

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General Introduction

"It is somewhat more probable that our early progenitors lived on the African continent than elsewhere" (Darwin 1871, p. 171). This oft-quoted supposition is firmly engrained in the literature and minds of evolutionists or, more specifically, palaeoanthropologists. Indeed, fossil evidence does provide brief glimpses into the very vague process(es) of hominoid evolution, and as such helps to further entrench the notion that Africa is the "Cradle of Man". Such notions, while they have provided a focus and answers to debates on hominoid evolution and hominid origins, may have also unwittingly served as a filter of evolutionary thought and science. Referential importance is given to those tangible, physical facts which best suit the palaeoanthropologist's historically validated pre(mis?)conceptions. The end result is nothing short of bias.

Our preoccupations with African origins have lead to the discovery of tremendous amounts of information regarding hominoid evolutionary processes. However, these preoccupations may have unwittingly lead to the neglect of equally valuable and valid information from *outside* the confines of Africa. While Africa is invariably the birthplace of a more "advanced" stock of primates, i.e., hominoids, increasingly evidence supports that certain factors of Miocene climate, geography and ecology would have made Africa a less than hospitable place within which neither middle to late Miocene hominoids nor early hominids could have successfully lived and evolved. Therefore, it may be more fruitful for palaeoanthropologists to extend the study of hominoid evolution and human origins beyond Africa to, in turn, consider inter-continental dynamics (i.e., climate, geography, ecology, etc.) and the moderating effects such factors have had on population dynamics and evolution.

The focus of this thesis is to adopt a broader, more encompassing perspective in relation to the evolutionary study of humans and their most likely progenitors, the Miocene apes. The aim of this paper is not to disprove long-held ideas, facts or fallacies regarding the role played by the African continent in regards to hominoid and hominid evolution. Rather the goal is to take a more expansive look into the *how*s, *when*s and *why*s of hominoid evolution. More specifically, evolving hominoids will be studied from the perspective that they are active participants within and respondents to an ever-changing suite of environmental/ecological circumstances. The analogy to be drawn throughout the thesis is one wherein evolving hominoids are the players of a on-going play. Certain features of the setting (i.e., the palaeoenvironments) and plot (i.e., the cyclic and predicable nature of primate adaptation and evolution) are key to understanding each of these players and their "on-stage" inter-dynamics.

The fundamental ideas and principles of ecology will be developed as they are essential to a fuller understanding of the setting and plot of which evolving hominoids were/are inextricably a part. The notion of ecology was first introduced into the general world of science in the 19th Century. At the turn of the century the inherent ideas of this scientific approach were to become widely employed, but only insofar as they served as valuable supplements to biological science and inquiry. It was not until much later (the 1960s) that ecology gained increased recognition as the valid and worthy "... branch of science ... most relevant to the everyday life of every man, woman and child" (Odum 1971, p. 3). In all areas of science, including anthropology, the value of ecological study is found in its multifaceted - multi-disciplinary mode of inquiry. Ecology is not a simple, linear science. Rather, it is a multidimensional discipline espousing the ideas and principles of such varied sciences as biology, natural history, climatology, geography, biochemistry, physiology, and behavioural science (Begon *et al.* 1996, p. vii). It is this tremendous scope of ecology that makes it of great utility for anthropological research. More

specifically, its synthetical nature allows for sometimes scarce and otherwise unrelated information to be conjoined towards the end of devising a bigger, clearer picture of things past - such as is the quest of palaeoanthropologists and palaeoprimatologists alike. This thesis will endeavor to reveal the tremendous and varied insights the science of ecology can provide in relation to the rhyme and reasons of hominoid evolution.

The first chapter will provide a general introduction to the basic principles of ecology. An emphasis will be placed on introducing and defining the process of "Ecosystematics", or the dynamic and cyclical relationship between factors of ecology and evolution. Chapter Two will specifically apply these basic ecological ideals and principles to palaeoanthropological and primatological inquiry. General trends in hominoid adaptation and evolution will be paralleled to broad changes evidenced to have occurred in palaeoecology and palaeoenvironments. Chapter Three will provide a specific overview of key adaptations manifest by the key "players" in hominoid evolution. The final chapter will provide a synthesis of all previously discussed information.

In looking both within and beyond the limits of Africa, attention will be given to changing climates, ecosystems and geography throughout the Miocene in an effort to reveal how such changes/trends invariably contributed to hominoid migration and subsequent evolution. It will be shown how cycles of competition, niche differentiation and exclusion, as aggravated by climatic, palaeoenvironmental and ecological cycles, were the impetus behind hominoid migration events, adaptations, and evolution. The synthesis of such diverse information, as made available through such an ecological approach, will help to define the patterns and processes of hominoid evolution throughout the Miocene. Further, it is hoped that such information will help to pave a more solid path which will lead future studies regarding hominoid evolution and, ultimately, hominid origins out of Africa and into less well-charted, but equally as relevant areas - namely Eurasia.

Chapter One

Creating a Backdrop: Aspects of Ecology and Evolution

"No organism can exist by itself without an environment" (Odum 1971, p. 8). Indeed, for even the simplest life-forms the security of short term (individual) and long term (species) survival, is found only when a complex and delicate balance is struck between the biotic and abiotic realms of the environment. The science of ecology seeks to explain and define this dynamic, delicate relationship between organisms and their environment. As with the ecologist, of interest to the palaeoanthropologist is how organisms lived in their past surroundings. However, in going beyond the scope and study of ecology, the palaeoanthropologist seeks to understand not only how individuals and species survived within their environments, but also they adapted to and evolved in response to these changing environments. Because the aim of this thesis is to explain and substantiate the probable mechanisms behind hominoid/hominid evolution, and because such mechanisms are very likely borne of environmental circumstance, it is first essential that one understands the fundamental principles of ecological dynamics, from both a spatial and temporal perspective. In this and subsequent chapters it will become apparent how such principles can be used to help reveal valuable clues regarding the environment(s) in which primates participated and evolved.

In this chapter the science of ecology will be explored. First the boundaries of ecological study will be defined. The crux of discussion will be on developing a basic definition and understanding for the new term "Ecosystematics". The ideas unique to Ecosystematics are those which bridge together aspects of space (i.e., ecology and the immediate environment) and time (i.e., evolutionary processes in a palaeoanthropological context). As will be seen, the relationship between organisms and their environments is of tremendous complexity, both in space and over time. The ideas of Ecosystematics help to

delineate the complex web and cycle of proximate *and* longterm changes in an ecological context. Because of the dynamic and complex nature of both ecology and evolution, a clear understanding of Ecosystematics is best achieved, not by means of a linear methodology (i.e., focussing on one problem, result or conclusion), but rather by embracing a multi-dimensional and multi-directional approach wherein it is readily recognized that "everything effects everything else" (Begon *et al.*, 1996, p vi). The first portion of this chapter will review the various and interwoven stages of the process of Ecosystematics. The final section will focus on the varied ways in which the participants of an ecosystem (i.e., communities, populations and individuals) respond and adapt to, and ultimately evolve in conjunction with fluxes in the Ecosystematic process. Such an understanding of Ecosystematics, will be of great utility to this thesis' aim of substantiating processes of hominoid evolution and the implications they hold for Eurasian hominid origins.

Ecosystematics: The Interplay of Energy,Organisms, Environment and Evolution

As mentioned, ecology is simply the study of the relationships between organisms and their environments. For the ecologist the key unit of study is the ecosystem which, in its essence, is the observed dynamics (obligatory relationships, interdependence and causal relationships) of organisms and the environment. As Odum (1971, p.8) develops and defines:

> Living organisms and their non-living (abiotic) environment are inseparably interrelated and interact upon each other. Any unit that includes all of the organisms (i.e., the "community") in a given area interacting with the physical environment so that a flow of energy leads to a clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and non-living parts) within the system is an ecological system or *ecosystem*.

Fundamental to the proper functioning of an ecosystem is the regular and even flow of energy throughout the system (Begon *et al.* 1996; Odum 1971). The importance of energy and energy transfer within an ecological setting was first recognized and developed through the works of A.J. Lotka (1925) (see also Odum 1971). Following the basic Laws of Thermodynamics, it is known that energy can neither be created nor destroyed, only transformed (First Law of Thermodynamics). However, most instances of energy transformation within a system, in this case the ecosystem, fall short of complete efficiency. This tendency towards inefficiency is referred to as the Second Law of Thermodynamics, or the transfer of energy to a more dispersed, and hence, less accessible state. Within an ideal ecosystem, proper functioning and maintenance are achieved when the internal order of the system is kept at a maximum through energy consumption, while disorder (entropy) is kept to a minimum through the continued release of energy (Odum 1971).

In a terrestrially- based ecosystem, the ideal energy balance is struck under conditions where the resource base (biomass) is sufficient to support the consumer base and, in turn, where the energy/resources consumed are efficiently redistributed into the environment (i.e., energy transformation). The pioneering work of Lindemann (1942) introduced and defined the highly complex, hierarchical interrelationships and structures which underlay biotic communities. In essence, Lindmann was the first to delineate the structure and dynamics of the *Trophic Pyramid.* Essentially, it is through this trophic structure that energy passes and, ulimately, through which an internal balance (or conversely inbalance) is established and maintained within an ecosystem. As Begon *et al.* (1996, p. 712) relate, within any given ecosystem the bulk of biomass takes the form of green plant material. As such, plant material is the primary producer of energy within a community or ecosystem. As the most consistent and largest source of energy, plant

materials form the base of the trophic pyramid. It is from this base that primary energy consumers (or the higher-order participants of the trophic structure) feed. In turn, energy passing through the primary consumer base is recycled and returned into the energy flow system. Therefore, these primary consumers (i.e., heterotrophs such as bacteria, fungus and animals) also serve as secondary energy producers within the ecosystem (Begon *et al.* 1996, p. 730).

Within a given environment all organisms, in order to compensate for certain limitations with which they are confronted (i.e., biomass and energy availability) will be forced to adjust their means of exploitation/behaviours and to re-structure their populations accordingly. A diagrammatic representation of the basic structure and the key constituent elements (i.e., the words/ideas highlighted in the text to follow) of all ecosystems can be found in Figure 1. Within an ecosystem, the fundamental and largest unit of study is that of the ***biotic community***. As Odum explains, the community is the living part of an ecosystem. In essence, the community is an aggregate of distinct groups, which together exploit and occupy a "prescribed area or physical habitat" (Odum 1971, p. 140).

A community, in turn, is composed of an array of ***populational groups*** or ***species***, all of which necessarily coexist in an orderly and structured manner. Populations within a community are best described as a collectivity of individuals generally believed to belong to the same or, at the very least, similar species (Begon *et al.* 1996, p. 965; Odum 1971, p. 162). What is important in defining a population is the fact that all members of a single population share a particular space or habitat within the larger ecosystem. Hutchinson (1957) was the first to study in detail how living things aggregate within and exploit the ecosystem of which they are a part. While the *habitat* of a population or species is simply the region it occupies, Hutchinson identifies a more finite area of occupation and

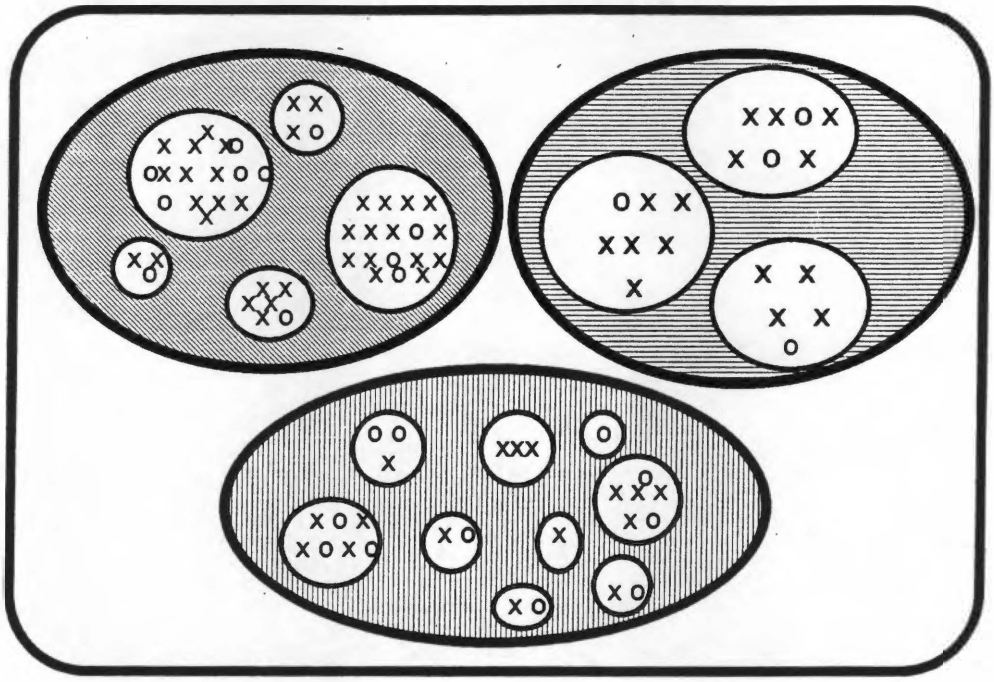


Figure 1. Ecosystem structure.

= **Ecosystem:** The interface of organisms and their environment.
Biotic - Abiotic Dynamics

= **Biotic Community:** An aggregate of populations and/or species occupying a specific biome or region of a biome within the ecosystem.

= **Populations:** Aggregates within the community of the same or similar organisms occupying overlapping and/or distinct niches.

exploitation, namely the *niche* of a population/species. The niche is not simply a passive setting that species occupy. Rather, the niche holds a dynamic and functional role in relation to both the population and the entire community. In fact, the niche exerts a certain amount of *active* control over the limits by which individuals are able to survive, grow and reproduce within their relatively passive habitat (Hutchinson 1957; Odum 1971, p. 234; Begon *et al.* 1996, p. 963). As participants and exploiters of a particular niche, populations demonstrate behaviours and attributes which "relate to their ecology, namely their adaptiveness, reproductive ... fitness and persistence...." (Odum 1971, p. 162). Such characteristics are unique only to that group/population.

Finally, populations are composed of ***individual organisms*** - the lowest and smallest units within the ecological structure. As will be developed further in a later section (Stage Five) individuals are the vessels in which characteristics unique to the population are (behaviourally and genetically) maintained and the means by which these same characteristics may be passed on to future generations of populations.

The dynamic nature of populational (re-)structuring and energy-flow within a community is directly linked to the trophic structure, or pyramid of productivity, specific to that community (Lindemann 1942; Begon *et al.* 1996, p. 731). In relation to those behaviours involving energy acquisition and consumption, all the same or similar populations will occupy a specific level within the trophic structure/pyramid - a level wherein they will directly participate in and contribute to the continued circuit of energy flow within the community. From one step of the food chain to another, energy is transferred to the end of sustaining all individuals within this trophic hierarchy. Ideally, the largest and longest sustained biomass will effectively support the largest community of individuals.

Direct observation and experience tells us that in the real world, and in actual ecosystems, the intricate and dynamic nature of the"web of existence" is such that an ideal

system, consistent with a long term balance of energy flow and biomass abundance, is rarely achieved. Variables, internal and external to the system, serve to disrupt the regular flow of energy and to steer the system towards increased disorder. However, within the ecosystem, as will become apparent, the role played by the energy consumer is *not* a passive one. For the majority of life forms the security of immediate survival and continued long-term existence depends not on passive functioning and energy consumption, but on the ability to compensate for, adapt to and ultimately evolve in response to the complexities of environmental change and potential disorder.

"Ecosystematics"

As outlined above, for the ecologist the fundamental units of study include communities, populations and organisms. The tendency among ecologists is to focus on the *immediate* interrelationships observed among these principal units within a given ecosystem. As Begon *et al.* (1996, p. vii) such a focus often "...ignores at its peril the details of the biology of individuals, or the prevading influences of historical, evolutionary and geological events". In contrast to the ecologist, palaeoanthropologists, while they may express some interest in the short, proximate dynamics of past communities (populations organisms, etc.), are much more concerned with those more long-term, ultimate dynamics (i.e., long term adaptations and subsequent evolution) of these past communities. The uniqueness and importance of Ecosystematics to palaeoanthropological inquiry is its combined emphasis on both the proximate (ecological) and, more importantly, the ultimate (evolutionary) variables which affect interorganismal dynamics. While an ecological study of the ecosystem may simply review the observed features and patterns within a spatially defined area, an Ecosystematic study looks in greater detail at how these features and patterns function in space and, more importantly,

over time, within a constantly changing system/cycle. It is the cumulative, cyclical process involving all circumstances of external systemic disruption, internal disruption, internal response and adaptation, and evolution that contributes to the idea of Ecosystematics. Figure 2 presents a schematic view of the ideas and dynamics fundamental to the process of Ecosystematics and can be used as a visual reference for the following discussion.

Stage One: Environmental Flux and Climate Change

As already inferred, an ecosystem is far from being a discrete or stable entity. As a system, it is of an amorphous nature, subject to continual change and modification due to external and internal influences. Of all observed ecosystems on earth, terrestrial ecosystems are among the most variable, fragile and susceptible to change. While many factors can affect the degree of stability in any given terrestrial ecosystem, three stand out as being of the greatest influence and importance. These are: 1) climate, 2) geography and 3) water. In reviewing Figure 3, what becomes apparent in relation to these three variables is the moderating affect that each has on the other and, in turn, on the ecosystem.

Climate: As Odum (1971) develops, on land temperature extremes are much more dramatic then in any other environments (i.e., marine). Global and regional climate trends logically impact the amount of solar radiation and moisture available to the biotic communities within a given ecosystem. As such, climate and the restrictions it imposes on light and water determine the development of regional biomass (resources). Consequently, these climate-induced restrictions will define the number, kinds and trophic structuring of any organisms able to participate in that ecosystem. As Begon *et al.* (1996, p. 896) relate, organisms will tend to adapt to/specialize within a certain trophic level of an ecosystem depending on the restrictions imposed upon them. Invariably, changes in

"Ecosystematics"

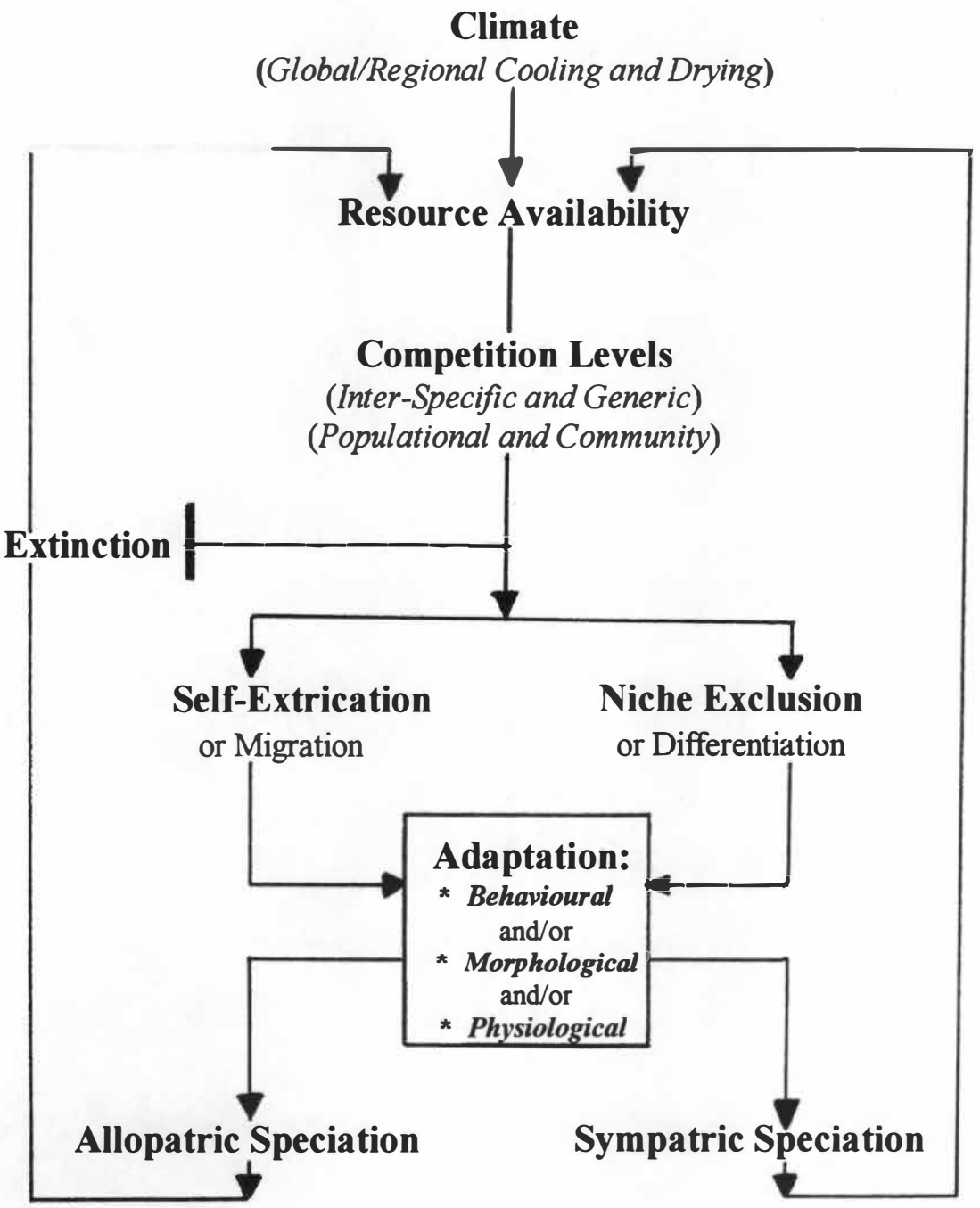


Figure 2. Ecosystematics

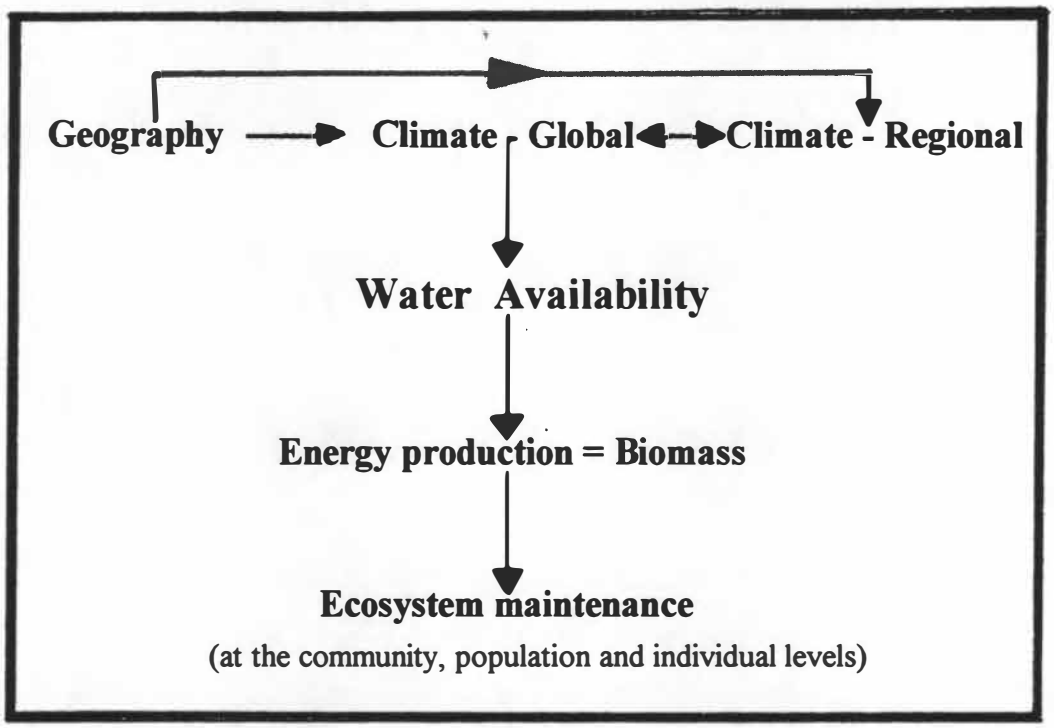


Figure 3. The interrelation and impact of climatic variables on "Ecosystematics" Stage One

climate and the subsequent alteration in moisture, light and biomass levels will have an effect on the structure and function within the system - thereby disturbing the system's normal internal energy flow (see also Lindemann 1942; Begon *et al.* 1996, p. 712).

Geography: "Land, unlike the ocean, is not continuous; there are important geographical barriers to free movement" (Odum 1971, p. 363). The obvious, proximate effect of geographical barriers on living terrestrial ecosystems is the pronounced segregation of these ecosystems in distinct, regionally-bound biomes, or plant assemblages, and animal communities. In addition to immediate geographic circumstance, over a greater time-span and from a more global perspective, geography and geological transformations (i.e., episodes of tectonic up-lift and volcanism, etc.) will have a significant effect on the functioning of ecosystems (Malone 1987; Begon *et al.* 1996, p. 4). The formation of new, more expansive mountains and other topographical

formations will interfere with the already established spatial placement and boundaries of existing biomes and animal aggregates. While, through the production of barriers, geographic transformation can serve to circumscribe biomes and communities, it can conversely help merge biomes and biotic spheres by establishing "bridges" between otherwise separate ecosystems.

In addition to altering the physical structure of the environment, geological transformations can further effect the ecosystem by impacting global and regional climatic patterns. The greatest repercussions of geographic transformations are typically felt in relation to the hydraulic cycle and water availability. Over the course of the planet's geological history, doming and rifting has resulted in numerous such climatic changes. In many instances, geographical perturbations (such as those changes induced by the "rain-shadow effect") have contributed to regional reductions in preciptiation rates and the subsequent increase of environmental desiccation (Malone 1987; Boaz 1994).

Water: As seen above, water availability within an ecosystem is moderated by both climatic and geographic variability. In sum then, water, as the defining criterion of both plant and animal life, is critical to the proper functioning of and efficient energy flow within an ecosystem.

Each of the above three variables of climate, geography, and water is of significance to the other, and when taken together they contribute to the first stage of Ecosystematics, namely that of climatic variation (i.e., cooling and drying). In relation to major trends in hominoid evolution, it is generally held that climatic change throughout the Miocene, Pliocene and Pleistocene has been marked by numerous oscillations in global and regional climates. However, from the latter stages of the Miocene onwards, the overall trend was towards progressive, global and regional episodes of drying and cooling. As will be discussed in more detail in subsequent chapters, it is generally held that throughout all the major epochs of hominoid evolution "climatic change" (i.e., Stage One in the

Ecosystematic cycle) has, in varying degrees, influenced the mode and tempo of hominoid evolution (Pickford 1983; Kortlandt 1983; Vrba 1985, 1995; Malone 1987; Coppens 1989; Roberts 1992; Boaz 1994).

Stage Two: Resource Availability

Factors of biomass/resource availability are integral to the second stage of Ecosystematics. As already discussed, within an ecosystem a balanced and optimal energy flow is achieved when the amount of energy consumed is matched by the amount of energy dissipated, and ultimately, when the maximum efficiency for each is reached. Regional variation of biomass availability will directly affect community structure as well as population dynamics, diversity and size (consult Figure 4). The ideal ecosystem, wherein the greatest biomass is accessible to the greatest number of species, is an ecosystem which is best approximated by the conditions of a tropical biome (Unit 1 of Figure 4). Within a tropical rain forest ecosystem, a very large biomass can be maintained. Where resources are in such abundance, the fundamental niche of a species (i.e., all possible resources available for consumption) and the realized niche (i.e., only those resources available after competitors are taken into account) may be virtually indistinguishable (Hutchinson 1957; Begon *et al.* 1996). The abundance and diversity of potential energy resources within the tropical rain forest allow for very speciose communities. In these biomes, where resource stability is in evidence, species diversity within a single community can potentially reach its maximum levels (Odum 1971, p.149). In such ideal circumstances, species diversity and survival is guaranteed by virtue of the fact that there is "more than enough to go 'round". Indeed, these resource patches of plenty allow for many species to access a more than adequate supply of energy-rich resources. However, the very speciose nature of these ecosystems is such that resource

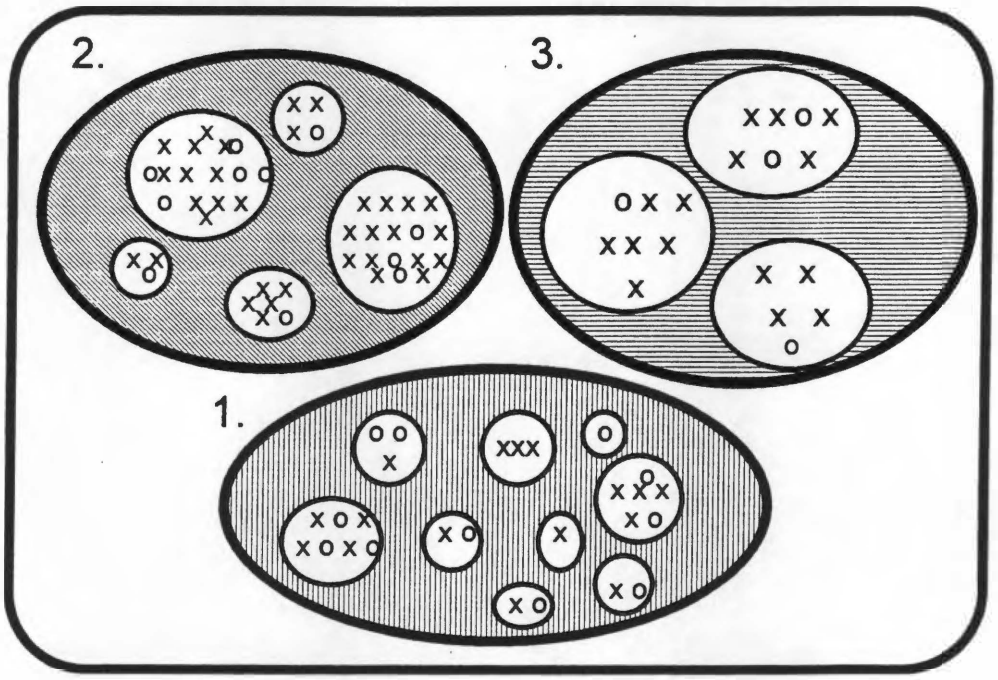


Figure 4. Biome structure.

1. = Large Biomass (i.e., tropical biome) supports many distinct populations (high species diversity). Each population contains only a few individuals.

2. = Intermediate biomass (i.e., temperate biome) supports an average level of species diversity. Each population can support a greater number of individuals.

3. = Small biomass (i.e., desert or arctic biome) supports only a limited number of species. Rigorous and depleted environments can support only a few individuals.

diversity need not equate to absolute and constant resource *availability* over time and space. In other words, while plant (and other) resources may be numerous in kind, the actual number of each kind is usually few. Within a given ecosystem, each consumer group will have specific food preferences. However, these resources may be restricted over space in terms of their absolute availability. Ultimately, then, each consumer group will necessarily have to be small enough so as not to over-exploit their specified resource preferences or to over-exceed the carrying capacity of their niche. As such, population sizes tend to be restricted/small in tropical biomes, in spite of resource diversity (Odum 1971; Begon *et al.* 1996).

Unfortunately, the earth's history repeatedly shows that tropical forest, although rich, are not "forever". As Odum explains, "(the) larger the biomass, the greater the maintenance cost" (Odum 1971, p. 39). Tropical forest biomes do house immense quantities of potential and realized energy. But the vulnerability of such stored resources is inextricably tied to the biotic requirements of large and constant supplies of sunlight and moisture. Minor perturbations in seasonality and/or more severe alterations of global and regional climatic conditions can quickly and seriously disrupt the balance of energy flow within the tropical ecosystem.

Unit 2 of Figure 4 reveals the structure of a community experiencing a certain degree of stress and instability in relation to biomass production and energy availability. Biomes occupied by such communities might include deciduous forests, coniferous forest, woodland and savannah environments, to name a few (Begon *et al.* 1996). Less diverse and resource-restricted environments would ultimately result in a lower energy output on the part of primary producers (i.e., a smaller plant biomass). The lower density, higher dispersal and greater infrequency of available resources in such biomes would impact the level of species diversity. Generally, in regions subjected to physical controls (i.e., environmental and climatic stress) species levels are directly proportional to the number of

niches and resources available for exploitation (Odum 1971, p. 149). While species diversity may be low, there is a tendency for the size of each species population to be large (at least larger than those sizes observed in a tropical biome).

Extremes in physical controls exerted on an environment, such as in an arctic or desert biome, will result in severe reductions in biomass availability (Begon *et al.* 1996; Odum 1971). As Unit 3 in Figure 4 demonstrates, both species diversity and population densities are correspondingly low. As would be expected, the energy flow within this type of ecosystem is limited in its efficiency. The trophic structure is limited to only a few species vying for limited amounts of resources/energy.

In the above description of three eco-types, it should be apparent that community structure is dependent on and, therefore, defined by the overall availability of resources. Resource availability, in turn, is highly dependent on climatic flux and water availability. Any reduction in levels of water for the plant community, invariably leads to an imbalance of the trophic structure at its roots. A reduction in plant availability will invariably lead to a decline in the number of animals reliant on the plant biomass for their survival. Any reduction in lower-level (i.e., close to the bottom of the trophic pyramid) consumer group numbers will ultimately impact each successive level of the trophic hierarchy.

Stage Three: Competition

Reduced levels of resource availability and niche space ultimately leads to the third stage in the process of Ecosystematics, namely increased competition. A general principle of ecology, Gause's Rule (as will be discussed in the following section), maintains that no two species can occupy the same niche (Odum 1971, p. 218). As resource richness begins to decrease in response to climatic flux and environmental degradation, the realized niche of a species will subsequently be reduced. In addition, as potential habitats become less abundant and increasingly circumscribed, a species' realized niche will be further

reduced as a result of increased competition levels brought upon by encroaching populations and niche overlap.

While the proper functioning of an ecosystem depends on a balanced internal dynamic between communities and populations, the continued maintenance of these communities, populations, and the entire ecosystem depends on the survival and success of the participant individuals. Indeed, in this case, the parts make up the whole. Threats to the security and stability of the individual ultimately effect the entire ecosystem. For this reason, it is essential to understand the cause and effect relationship inherent between competition and the individual.

Fundamental to successful competition is the ability of the individual to access a sufficient amount of resources, hence energy, to ensure its own immediate survival . The Optimal Foraging Theory (OFT) is frequently and successfully employed as a means of understanding and explaining the relationships foraging behaviours, resource acquisition and survival/fitness in terms of cost and benefit equations (Pyke *et al.* 1977). As Pyke *et al*. develop, the aims of such theory are to predict and explain patterns of animal behaviour through the application of simple mathematical models which equate an animal's diet and net rate of energy intake to the animal's immediate survival and long term success (i.e., fitness). The optimal diet is one in which the net energy intake exceeds that of energy expended in confronting and overcoming certain obstacles and limitations of the environment (i.e., those impeding resource allocation times, handling times, consumption, etc.). Excessive levels of resource competition invariably tends to increase the energy required for resource acquisition and, consequently, will tend to decrease the likelihood of maintaining an optimal diet.

The *proximate survival* of a species, as secured through energy procured via the optimum and preferred diet of that species, is only guaranteed insofar as the entire collection of individuals within the species/population is able to carve out and monopolize

a niche within the ecosystem. Such a monopoly is only achieved when the population group acquires a shared, unique and, most of all, successful repertoire of foraging behaviours. In a balanced ecosystem, a niche occupied/exploited by one population/species should maintain a complementary position in relation to other groups. By complementary, it is meant that the activities and behaviours of one species should not directly or adversely interfere with the behaviours of any other species occupying spatially close or functionally similar niches. Odum defines such a relationship as one of "neutralism" (Odum 1971, p. 211). Rates of energy consumption and energy exchange tend to exhibit a regular flow under such circumstances. Indeed, such uniform and balanced conditions cannot occur in instances of environmental competition and stress. The effects of competition, as they can and do serve to limit the optimal diet, will effectively alter the structure and stability not only of the individual, but of the species, the population and even the community as a whole. As Begon *et al.* (1996, p. 265) explain, such effects will have both proximate and long term (evolutionary) implications:

> The essence of interspecific competition is that individuals of one species suffer a reduction in fecundity, survivorship and growth as a result of resource exploitation or interference by individuals of another species. The competition is likely to affect the population dynamics of the competing species, and the dynamics in turn can influence species distributions and their evolution. Of course evolution, in *its* turn can influence the species distributions and dynamics.

Minor perturbations within an ecosystem, such as those induced by the combined effects of geological, climatic and hydraulic fluctuation, can and often do result in an imbalance of the internal energy flow and trophic structure of a community. Such an imbalance will be rooted in the variable production of biomass within the environment. The end result would be an inverted pyramid in relation to the normal trophic structure of the environment (Odum 1971, p. 81). Originating and moving upwards from the base of the food chain (i.e., plant life), the adverse effects of an internal imbalance and an increase in competition will be felt, in varying degrees, by all species of the ecosystem

whose proportionate numbers and energy requirements in relation to a decreasing biomass would be extreme and, in some instances, insupportable.

Environmental disruption/variability is thought to have a differential affect on species depending on their modes of adaptation (refer to Figure 4). Stenotypic species are those which evidence the greatest degree of specialization in relation to their behavioural and morphological adaptations to habitat use, food acquisition and overall niche exploitation (Price 1996; Odum 1971). Within most ecosystems or specific biomes, stenotypic species tend to be under- represented in the population (Odum 1971, p. 139). As Price develops (1996), because of the finely-honed adaptations and meager representation of this species type, "steno" species are more vulnerable to and demonstrate a greater intolerance of disturbances involving niche space, resource distribution and variable competition levels. Consequently, stenotypic species tend to undergo rapid and definite niche differentiation. Under conditions of tremendous environmental stress, niche differentiation frequently results in spatial isolation and subsequent allopatric speciation. As such, stenotypic species tend to be more speciose, over both time and space.

In contrast to stenotypic species, eurytypic species are less susceptible to environmental change. The behavioural and morphological characteristics of this species type are such that environmental shifts are compensated for by means of a generalized and flexible mode of adaptation. As Price (1996, p. 213) defines, the eurytypic types are essentially those "...species and lineages with broad food and habitat tolerances and utilization patterns, spreading their foraging over more than one biome". Typically, although not exclusively, eurytypic species compose the majority of an ecological community (Odum 1971). As Price (1996) further explains, while population numbers tend to be large among these generalists, the occurrence of speciation events, and hence overall species' diversity, is relatively low. Further, while euryspecies are not exempt from the processes of speciation, their generalized behaviours and morphologies facilitate

immediate responses and adaptation to alternations in their occupied niche. Consequently, the generalized behaviours and morphologies tend to reduce the frequency of extinction and speciation events among such eurytypic species.

Stage Four: Responding to Competition

Numerous studies have been conducted with regards to the effects of resource and niche stress on levels of inter-populational/specific competition (consult Begon *et al* 1996). Among the most relevant to ecological thought and theory are those conducted by G.F. Gause (1934, 1935). Gause, in his studies, noted the differential abilities of separate species (in his experiments species of protozoan *Paramecium*) to live in shared and/or overlapping niches. For some species, the result of shared/overlapping niche space was the replacement of one species by another and, ultimately, the extinction of at least one of species. By contrast, for other species, niche overlap, while it did result in a decrease in populational numbers for all species involved, did not result in obvious episodes of extinction and replacement. Instead, each species appeared to undergo niche separation as means of avoiding excessive niche over-lap and competition.

Today, Gause's Principle is essentially synonymous with the principle of Competitive Exclusion. Begon *et al.* (1996, p. 959), summarize these principles of competition and exclusion as follows:

> The idea that if two competing species coexist in a stable environment, then they do so as a result of differentiation of their realized niches; but if there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other.

From the above citation, it is apparent that species are much more than passive objects of environmental circumstance and change. Indeed, as direct participants they are able to adapt to environmental flux and competition. Means of responding to increases in

resource depletion and interspecific competition can include: 1) extinction, 2) niche differentiation, or 3) niche exclusion and subsequent migration. Each of these three responses involve some degree of behavioural or morphological adaptation (Refer back to Ecosystematics diagram, Figure 2).

The first response listed, extinction, is by far the most extreme of the three. While survival is ensured by the overall capacity to respond to new problems within the set physical and social environments of organisms and their populations, extinction is the consequence of failing to meet and over-come such problems (Foley 1984, p. 93) Conditions of extreme environmental stress provide the perfect circumstances for extinction events. Under intensely stressed circumstances, the abilities of the individuals/species to actively monopolize resources and energy necessary for survival are extremely restricted. Consequently, the behavioural abilities and morphological capacities are rendered insufficient/inefficient. The immediate result is the halting of energy-flow to this consumer group. Ultimately, a species extinction results from the inability of the individuals to pass on genetic fitness to future generations.

Niche differentiation is the second response. Following this means of response, species remain in their original environment and attempt to maintain a certain degree of control/exploitative power over their realized niche. Interspecific competition is kept to a minimum insofar as realized niches of competing species are not identical. While *habitats* of sympatric species may be indistinguishable, *niches* may be only partially overlapping if at all (Odum 1971, p. 236). Behavioural adaptations are key to such responses, and might include variations in: 1) the resources chosen/preferred for consumption, 2) the principle resource patches exploited, 3) modes of exploitation, 4) times of exploitation, etc. (Clutton-Brock 1977; Cant and Temerin1984; Begon *et al.* 1996). Adaptations of a more long term impact (i.e., genetically acquired and passed) can ensure a more successful co-existence of two species (Begon *et al.* 1996, p. 295). Character displacement, or the

modification of morphological/behavioural traits, can help to reduce levels of competition and, further, will help to maintain or enhance a species distinctiveness and ultimate success (Odum 1971, p. 240).

The final response associated with excessive interspecific competition is that of niche exclusion, both forced and voluntary. This response comes as a result of one species' inability to secure its dominance/monopoly over its former, realized niche. As such, the less successful species no longer holds a defined role within its given environment. Survival of this species depends on its ability to secure requisite resources and energy from *outside* its typical niche. If a new niche is similar to or the same as the former niche, behavioural and morphological adaptations may not be significantly altered by the process of self-extrication or forcible displacement from one environment to the next. Subtle differences associated with the new environment can, however, prompt some behavioural modifications. More severe variance will tend to result in long term (genetically acquired and passed on) morphological variation.

Stage Five: Species Evolution ... and Back to the Beginning

Proximate adaptations can and do persist over time as long-term, evolutionary adaptations. As briefly touched on in a previous section (i.e., Stage Three: Competition), it is at the level of the individual, and possibly even at the level of the group/population, that both degrees of proximate (ecological) and ultimate (evolutionary) success may be determined. At any given time, within a community/group there usually exists a marked degree of variablity, both behaviural and morphological, among all individuals. While a great majority of these characteristics will be of little benefit to an individual in its efforts to secure its immediate and long term survival (i.e., neutral mutations and/or retentions), some may prove to maximize the individual's chances of survival (Darwin 1859). Within the ecological setting, those characters of immediate benefit will be those (relating to

resource aquisition) which help to ensure that the individual maintains a monopoly over a certain niche and, consequently, that the individual continues to maximize its energy intake. Some characteristics/traits (of negative, neutral or beneficial influence) possessed by an individual (or individuals) may be of heritable value. Over time and generations some of these traits will be retained while others are lost. In addition, some of these traits will prove to be of use and others of disuse. From this range certain traits, as they persist among individuals, may prove to be of adaptive significance/advantage insofar as they promote a maximization of fitness for the individual - a fitness which will likely be passed on to other, future generations (Darwin 1859; Pyke *et al.* 1977; Begon *et al.* 1996). In sum, under circumstances of environmental stress and change, variations may be present within the population (i.e., as manifest in the individual) which lead "... to an adaptive improvement, placing an individual at a selective advantage within a population. As a result of the reproductive benefits that this confers on the ... (individual, such adaptations) ... will spread through the population and consequently an improvement may be said to have occurred" (Foley 1984, p. 92).

As the previous section supports, the means by which species/populations respond to changing environments are varied. Each of these responses, in turn, contributes to the cycle and process of Ecosystematics. The absolute inability of a given species to adapt to or cope with ecological change and circumstance will ultimately lead to the extinction of that species. With the extinction of a species, so ends the evolutionary stage of the Ecosystematic cycle. While the extinction of one species may tend to stop the cycle of Ecosystematics *for that species alone*, niche differentiation (or sympatric speciation through character displacement) and niche exclusion (or allopatric speciation through spatial and temporal separation) will help to ensure that this cycle is brought full-circle. In light of imposed ecological stresses, individuals, if they are to persist, must necessarily respond to and adapt to those problems which pose real and immediate danger to their

existence. In the short term as niches become unique or entirely separate, behaviours may be modified and some physical attributes will become of realized, immediate utility for the individual under circumstances of adversity. Over evolutionary time, the genotypic manifestations of those most beneficial phenotypic and behavioural traits may be selected for and passed on through future generations. Those who survive will be those who again will respond to *new* and different variables in the ecosystem, if and when they occur. Hence, the process of Ecosystematics begins again.

As the above discussion has shown, the ecosystem is a complex web of cause and effect. Adaptation and evolution come about in response to unique problems posed by variable environments. Ecosystematics synthesizes evidence of an evolving environment (i.e., climate, resource availability and competition) and of simultaneously evolving biotic worlds. Delineating and explaining certain trends and relationships observed to exist at and between all stages of the Ecosystematic cycle (i.e., climate change, resource availability, competition, adaptation and evolution) will make the task of interpreting the palaeoecological, palaeoprimatological/anthropological records that much easier. The next chapter will approach these variables of ecosystematics from the specific perspective of primate evolution. In doing so, it is hoped that the stage will be set for a clearer conceptualization of the processes behind hominoid and hominid evolution.

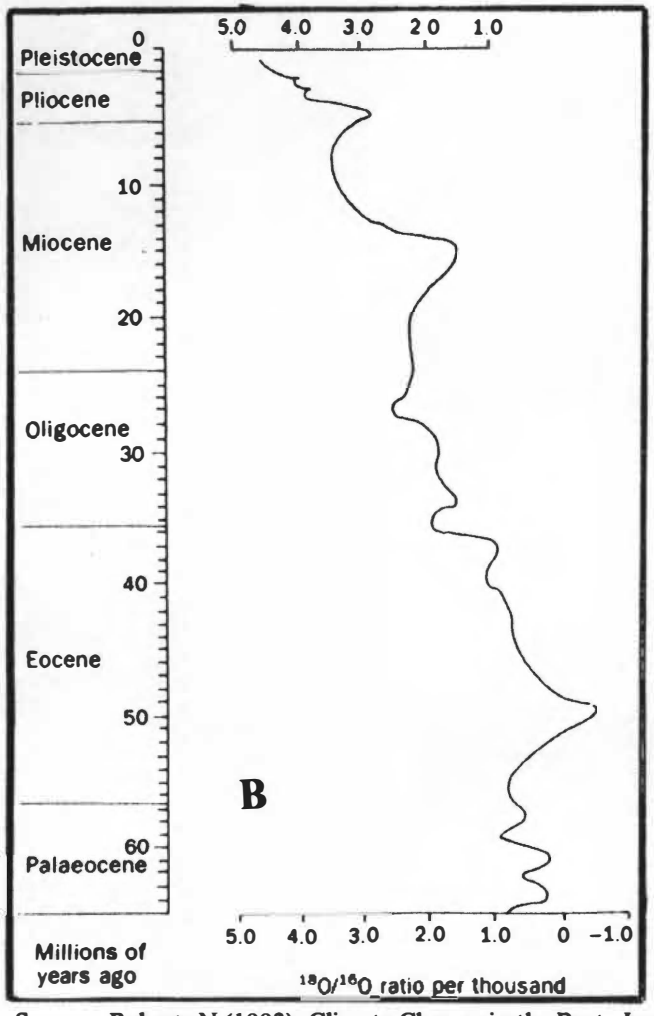
Chapter Two

Developing the Plot: Ecosytematics from a Palaeoprimate-Perspective

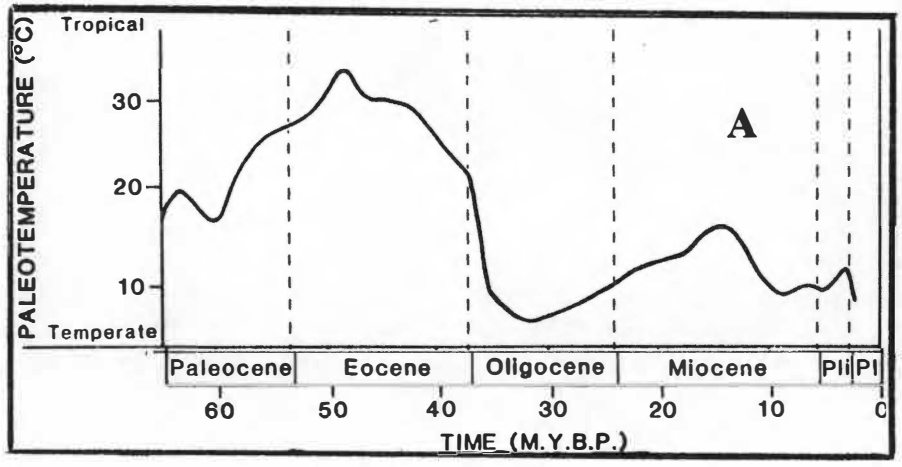
This chapter will explore how the ideas and principles of ecology have been and will continue to be of tremendous utility to studies of primate evolution. The backdrop of hominoid/hominid evolution (as a combinations of both theory and fact) will be constructed. Each stage of the Ecosystematic process will be explored with specific attention given to pertinent ideas of primate behaviour, adaptations and evolution. Through such exploration, the importance and applicability of Ecosytematics to the cycle and trends of hominoid/hominid evolution will become apparent.

Climate

Climatic events and trends have long been upheld as some of the primary determinants of primate, including both hominoid and hominid, evolution (Napier 1969; Kortlandt 1983; Tchernov 1992; Coppens 1988/89). Throughout all the major epochs of primate evolution (i.e., the Palaeocene through to the Pleistocene) many observed climatic shifts are known to have occurred. As Figures 5a and b demonstrate, since the Palaeocene, numerous oscillations mark the history of primate palaeoclimatic conditions. Figure 5a provides a very basic schematic view of temperature variation throughout these epochs. As Roberts (1992) explains, shifts and patterns of palaeoclimates, although not directly measurable, are often correlated to shifts in oxygen-isotope ratios (O18:O16) as are measured from fossilized foraminifora in deep-sea sediments. Generally, it is found that under conditions of higher global temperatures, the precipitation of O18 tends to be somewhat less than that of O16. During periods of intense global cooling (i.e.,



Source: Roberts N (1992) Climate Change in the Past. In S Jones, R Martin and D Pilbeam (eds.): *The Cambridge Encyclopedia of HumanEvolution.* Cambridge: Cambridge University Press, p.176.



Source: Fleagle J (1988) Primate Evolution and Adaptation. San Diego: Academic Press, p. 261.

Figure 5. Measures of climatic variability from the Palaeocene to Present. A = Average palaeotemperatures from the Palaeocene to present. B = Oxygen Isotope measurements from tropical deep-sea foraminifera from the Palaeocene to present.

glaciation events) the preciptation of O18, and hence the oxygen-isotope ratio, will be greater (Roberts 1992). As Figure 5b demonstrates, oxygen isotope measures do reveal significant oscillations throughout the course of primate history. Throughout the major epochs of hominoid evolution, namely from the terminal stages of the Oligocene through to the Pleistocene, there have been numerous, minor fluctutations in oxygen isotope ratios indicating frequent shifts from cooler to warmer, and wetter to drier conditions (and vice versa) (Tchernov 1992; Roberts 1992; Hill 1995; Opdike 1995; Vrba 1995; White 1995). However, as Figures 5 a and b clearly show, the cumulative effect of all climatic shifts during this time period has been that of an overall cooling and drying, with marked episodes of cooling/drying occurring during the mid to late Miocene and Plio-Pleistocene.

From the earliest stages of the Miocene until the early middle Miocene, global temperatures were, on average, much higher than they are today (Nagatoshi 1987). Consequently, throughout Africa and Eurasia, the palaeoenvironments of the early Miocene were significantly different than those observed today. At this time areas of African tropical forest were significantly more wide-spread (Andrews 1992a, b). Within Eurasia, what are now temperate deciduous and coniferous regions were then lusher, sub-tropical biomes (Nagatoshi 1987). In fact, it is suspected that the limits of the sub-tropics extended itself northwards into Europe by 10-15 latitudinal degrees (Napier 1969). However, towards the end of the early Miocene, as increasingly larger quantities of the global water supply became locked in polar ice caps, the trend was towards cooler and drier climatic conditions (Napier 1969; Kortlandt 1983; Andrews and Van Couvering 1975; Andrews 1992a; Hill 1995; Nagatoshi 1987) (refer to Figures 5a and b).

Such change did not manifest itself abruptly, but rather was of a cumulative effect. In addition, the effects/outcomes of such change were not uniform in distribution. In Africa, climatic shifts resulted in an increasingly patchy distribution of tropical forest niches (Andrews and Van Couvering 1975). In Eurasia, while climates of the mid

Miocene still remained relatively warm and humid, the distribution of semi-tropical biomes declined and were gradually replaced by distinctly sub-tropical and temperate environments, all of which were marked by increased levels of seasonality (Napier 1969, p.63). During the latest Miocene, global climatic cooling, as manifest in the Messinian Crisis at 5.5- 6 Ma, reached its point of climax (Tchernov 1992). It has been suggested that by this time in the latest Miocene the distribution of most Old World climates and their associated biomes had achieved their current distribution (Cerling *et al.* 1993).

Geographical events have been of tremendous impact in relation to the course of primate evolution. Such events, in conjunction with global climatic shifts, have magnified regional trends of environmental desiccation. In east Africa, regional rifting, volcanism and doming throughout the Miocene and up into the Pleistocene has contributed to a measurable increase of seasonality and environmental heterogeneity (Malone 1987; Coppens 1989; White 1995). During the early Miocene of east Africa, levels of rifting and doming were minimal and had little effect on the uniformly tropical environment (Andrews and Van Couvering 1975). Subsequent uplifting during the latter half of the Miocene, however, was severe enough to prompt the creation of distinct rain-shadow areas, wherein conditions of extreme aridity were to prevail (Andrews and Van Couvering 1975; Malone 1987). Indeed, the effects of rifting and subsequent environmental dessication were most strongly felt within regions of east Africa, namely those areas to the *east* of the Rift System (Coppens 1988/89; Boaz 1994). In Eurasia, tectonic transformations throughout the Mio-Pliocene (i.e., the Alpine-Himalayan and Tauraus-Zagros mountain orogenies, the formation of the Red Sea rift) were also accompanied by significant shifts in regional climatic and environmental conditions (Tchernov 1992).

In addition to the compounded climatic effect that geographic transformations have had on regional palaeoclimates and ecosystems, it is important to make note of the ways in which these evolving geographic features have effected the dynamics and

distributions of communities and ecosystems. As Malone develops (1987), extreme regional variations in the climate and environment, as exacerbated by geographical circumstance, will keep communities apart. The formation of physical barriers such as mountains, oceans and deserts have repeatedly been shown through time to keep populations separate (Tchernov 1992). Conversely, tectonic movements, instead of pulling ecological communities apart, can merge them together through the formation of land bridges and other gateways (Thomas 1985; Tchernov 1992). Barriers and gateways alike have contributed to the mode and tempo of catarrhine evolution. How such tectonic movements and barriers effected migratory patterns of hominoids will be discussed in greater detail in Chapter Four. Figures 7 though 10 in Chapter Four provide a schematic view of how geographic variability, specifically in the circum-Mediterranean region, has impacted inter-continental dynamics (i.e, as related to climate, geography and floral/faunal shifts and migrations) of the Old World continents over the past 20 million years.

Resource Availability

As the above discussion has shown, climate (as a product of global meteorologic and geographical events) has been under constant flux throughout the course of primate evolution. In Chapter One it was discussed that within an ecosystem, variations in climate can and do effect the availability of water which, in turn, ultimately determines the levels of biomass and resource availability. As briefly mentioned above, during the early Miocene, east African ecosystems were associated predominantly with tropical biomes, or more specifically tropical, wet, evergreen forest regions (Andrews 1996). Rain-fall in such environments is typically very high, ranging from 80-90 inches a year (Begon *et al.* 1996; Odum 1971) Consequently, in such energy-rich ecosystems, a variety of resources is abundant year-round. Such resources are only minimally subject (if at all) to seasonal

variability and availability (Napier 1969; Begon *et al.* 1996). High-energy plants and insects are readily available and are, consequently, among the most highly sought after sources of energy among most tropical animals, especially primates. Such a demand for these resources makes their ready abundance (or even surplus) vital to the maintenance of such an ecosystem. These resources would invariably have been of tremendous importance to the typical Miocene hominoid's preferred diet.

As the Miocene of east Africa progressed, however, the regional effects of cooling and drying episodes resulted in the formation of an environmental mosaic. Such a mosaic consisted of an increased number of dry-adapted biomes including dry tropical and deciduous forests, as well as a higher frequency of woodland, grassland, savanna and steppe environments (Napier 1969; Pickford 1983). As with the conditions observed to exist to similar environments today, rainfall in such palaeoenvironments would have been significantly reduced to 60, or even as low as 10 inches per year (Odum 1971). In conjunction with a reduction in annual precipitation would invariably have occurred a marked shift towards increased seasonality and periods of intense seasonal drought (Begon *et al.* 1996). Such a change in the climate of east African biomes has been well documented in the observed shift from palaeoenvironments dominated by tropical (C3) plants to those dominated by a relatively high number of water-depressed, dry adapted (C4) plants (Morgan *et al.*1994; Cerling *et al.* 1991; Cerling *et al.* 1993; Kingston *et al.*1994).

A common misconception held about these environmental/ecological changes within the African ecosystem is that the shift from tropical to dry-open environments was quick and uniform. In fact, this was not the case. Up until the very latest Miocene east Africa was typified by ecologically diverse settings of which tropical forests still played a temendously important, although somewhat diminished, role (Kingston *et al.* 1994; Jacobs and Kabuye 1987). Such forests invariably continued to play an important part in relation

to hominoid and hominid evolution, for it has been within such forest-associated palaeoenvironments that most, if not all, hominoid/hominid fossil evidence has been found (Retallack 1992).

In Eurasia, the appearance of catarrhines did not occur until the close of the early Miocene (~18Ma)(Kortlandt 1983; Tchernov 1992). Hence, it is only during and after this time that the effects of climate and resource distribution/availability become of consequence to catarrhine, or more specifically hominoid, evolution. For the duration of the early Miocene and for the earliest stages of the middle Miocene (18-13Ma), central, western and the Mediterranean regions of Europe were dominated by a typically sub-tropical flora (Bernor *et al.* 1993; Nagatoshi 1987). The temperature and moisture levels in such subtropical regions would have been somewhat lower than those in of the tropical biomes. However, as in tropical biomes, degrees of seasonality, as generally attributed to of the sub-tropics, would have remained comparably low. In spite of subtle changes in annual mean temperatures and precipitation levels, resource abundance and distribution would have only been minimally altered. Consequently, resources would have continued to provide a consistantly accessible energy-base adequate for the sustenance of many different primate species. During this same time period, areas of the Middle East and Asia demonstrated a similar degree of sub-tropicality (Nagatoshi 1987). However, areas of Arabia and Turkey equivocally showed a tendency toward dryer and more open forested and parkland areas (Nagatoshi 1987; Tchernov 1992). Again, it must be kept in mind that the development in these areas of more dry adapted flora was not uniform. Further, the distribution of these new, more open and dry areas was not continuous. In fact, many extensive and continuous tracts of subtropical and marshy, tropical areas likely persisted (Nagatoshi 1983; Bernor *et al.* 1993).

Towards the close of the middle Miocene (12-13 Ma) the effects of global cooling and drying began to be felt in Eurasia. Overall, compared to conditions today, the flora

still evidenced a warm and humid climate. However, the subtropical floristic elements were gradually being replaced by plant life better adapted to greater seasonality, cooling and drying within the ecosystem (Nagatoshi 1983).

In general across Eurasia, the trend was towards more mosaic environments "...ranging from subtropical swamp forests (resembling parts of the Everglades in Florida) to moist, warm-temperate, oak-chestnut-pine forests (probably interspersed with glades), to open woodlands in a dry karstic landscape to savanna-woodlands with riverine forests in the African style" (Kortlandt 1983, p. 485). More specifically, from the middle and into the terminal and end of the late Miocene, subtropical forest were replaced by moist and temperate mesophytic forest, and were isolated to central Europe (Bernor *et al.* 1993). By the end of the Miocene, there was a more aggressive transformation within the ecosystems of Mediterranean Europe, the Arabian peninsula and southwestern Asia. These once subtropical regions became increasingly dominated by more open-country biomes - biomes wherein resources were invariably subject to greater fluctuations in seasonality (Bernor *et al.* 1993). In spite of the expansion of such open and arid regions, the persistence of pockets of warm and humid subtropical/temperate environments should not be discounted. Concentrated around water sources (i.e., marine coasts, lakes, marshes, swamps, rivers, etc.), these subtropical pockets would have served as potential resource/energy store-houses for a limited number of animal consumers (Nagatoshi 1987, p. 149).

As discussed above, it is apparent that the gradual trend in both Africa and Eurasia towards increased aridity greatly altered the availability of resources, both in kind and quantity, over time and space. The effects of resource depletion would have been great and varied for all animals within these changing ecosystems. Any restrictions to the energy supply would likely have favoured two extreme consumer groups: 1) those best able to specialize in response to dry and depleted environments (i.e., the stenotypic species

better adapted to dryer, more open spaces) and/or 2) those expressing the greatest flexibility in their responses to regional resource inconsistencies (i.e., eurytypic) (Odum 1971; Price 1996; Foley 1994). For all participants in these evolving ecosystems, the ultimate consequence of change could have been nothing short of intensified competition.

Competition

Attention has long been paid to the notion that ecological circumstance (i.e., climatic variability and resource abundance) is of direct consequence to the patterns and process of evolution among primates (see Napier 1969; Andrews and Van Couvering 1975; Andrews 1985a; Temerin and Cant 1983; Malone 1987). On a more specific level, much support has been given to the theory that environmental stress and variability was the prime mover behind the divergence between and distinct evolutionary trajectories followed by first apes and monkeys of the Old World (i.e., Andrews 1985a), and later colobine and cercopithecid monkeys (i.e., Jolly 1969; Napier 1969).

The general consensus maintains that the earliest higher primate forms of the Old World, as specifically restricted to the African continent, occupied lush and energy-riche tropical forest biomes (Andrews and Van Couvering 1975; Andrews 1992a, b). These early Miocene catarrhines are believed to represent, almost entirely, a primitive and fairly diverse stock of hominoids (Benefit and McCrossin 1995; Simons 1985; Andrews 1985a; Andrews and Martin 1987). While forms ancestral to Old World monkeys are known to have existed during the earliest Miocene in Africa their representation in the fossil records, in terms of both number and kind, is meager (Andrews 1985a; Pickford 1987c; Strasser and Delson 1987). All early Miocene primates, both monkey and ape-like forms, seemed to dominate the forest setting as adept arborealists (Rose 1994). To varying degrees, all of these early African primates shared distinctly monkey-like modes of locomotion which

were predominantly, although not exclusively, quadrupedal (Andrews 1992a). During the early Miocene, dental and other evidence has been said to suggest that both monkey and ape-like forms shared a diet based almost exclusively on ripe fruits (Fleagle and Kay 1985; Andrews and Martin 1991; McCrossin and Benefit 1994). While the niches exploited by all early primates overlapped, the ready availability of resources made competition among or between species rare if not altogether non-existent. Consequently, under such an ecologically and climatically equable setting, species diversity among the hominoids, and to a much lesser extent among primitive cercopithecoids, achieved great levels.

As mentioned, by the close of the early Miocene the negative effects of global and regional climatic cooling and drying episodes were gaining momentum. As a result, increased levels of environmental instability and regional diversity over-shadowed the once stable tropical forest niche. Dense, high-energy resource patches became fewer and farther between in their distribution and, as a result, niches once shared (entirely or in part) by numerous primate species became prime arenas of inter- and intra-specific competition. As a result, it is generally thought that hominoid and cercopithecoid species were to have come into increased and direct competition with one another for the same resources. The repercussions of restricted resource availability on African primate species diversity were great. Throughout the duration of the Miocene and through to the present day, the species variety among hominoids underwent serious decline while proportionally the numbers and kinds of monkey species increased dramatically. As Andrews substantiates: (Andrews 1985a, p. 53):

> Species diversity of hominoids is high in the early Miocene and decreases at a fairly steady rate during the middle and late Miocene. At the same time the diversity of species within single habitats also decreases from four to six species in the early Miocene to maximum values of three in the middle Miocene and two in the late Miocene and present.... The diversity of cercopithecoid monkeys is low in the early Miocene and increases at a steady rate (with an equal but opposite slope to the hominoid decrease) during the middle and late Miocene. Diversity within

single habitats increases from one species in the early Miocene to two in the middle and late Miocene and up to 8 in the present.

As will be discussed in more detail in a later section the ability of primate species to successfully respond to and compete within an energy-stressed environment has repeatedly been attributed to the short-term adoption and long-term evolution of unique and adaptive specializations (see for example Andrews 1985a; Temerin and Cant 1983; Malone 1987). As these authors would likely concur, in general, all primates, with their recognized and seemingly universal ability to respond to variable climatic and ecological parameters, are considered as eurytypic species. For the evolving hominoids, adaptations and specializations manifest themselves in a generalized way. As "eury-specialists" Miocene hominoids adopted distinct behavioural and some morphological specializations (i.e., those relating to diet and locomotion) which afforded them the opportunities to find and exploit resource patches unavailable to other cercopithecoid primates. Conversely, cercopithecoids appear in general to have responded to resource stress and competition by becoming more specialized. Specialized morphologies and feeding strategies allowed for the "same old" niches to be exploited in a variety of new ways. Throughout the late Miocene and into the Plio-Pleistocene, the increasing potential for greater conflict and competition within these cercopithecoid niches (i.e., colobine vs. cercopithecine) was likely countered by a further morphological specializations which not only allowed for the continued co-occupation or overlap of niches, but likely contributed to niche separation and higher rates of speciation (Napier 1969; Andrews 1985a).

Responding to Resource Stress

A shrinking resource base resulting from climatic/environmental deterioration, would seriously alter the individual and community dynamics within the changing ecosystem. As Malone (1987, p. 472) develops, "(the) combination of the fragmentation

of the environment ... would have created new ... pressures. To meet these pressures plants and animals would have to be able to remain in the shrinking moist areas, to adapt to the drier areas or to disperse between the moist areas". As discussed in Chapter One, there exist three possible responses to and outcomes of excessive competition within a given niche. These are: 1) extinction, 2) niche differentiation, 3) niche exclusion. Each of these, to varying degrees, has come into play over the course of primate, or more specifically hominoid, evolution.

Extinction: Extinction events appear to have an obvious and direct association with instances of extreme climatic instability, and the resulting instances of resource stress and local competition (Foley 1994). Estimates on levels of primate diversity suggest that, in assuming an average and constant rate of speciation since the Palaeocene, diversity levels of extant primate populations should be on the order of 6,000 species (Foley 1991). However, today extant species (a total of 180 primate species of which 150 belong to Anthropoidea) and fossil (250 "species") account for a very small fraction of this estimate (Fleagle and Kay 1985; Foley 1991). Similarly, estimates of hominoid diversity levels calculate that the current number of ape species should total 210, yet there are only 14 extant species and only slightly more fossil hominoid species known (Foley 1991). Given the above predictions it is apparent that episodes of extinction have been more prevalent compared to speciation events over the course of hominoid evolution. However, the fact that four ape and one human genera persist, attests to the fact that, somewhere along the line, environmental/climatic stress was met with successful adaptations and evolution.

Niche Differentiation: Provided that the resource/energy base is wide enough, many species can exist within a given habitat. However, as resource abundance becomes more restricted, each species, if it is to remain as a viable participant within the same resource area, must respond accordingly. As Clutton-Brock explains (1977) sympatric

primate species will necessarily respond to low resource availability by: 1) exacting ecological segregation, wherein regions/levels of the niche (e.g., heights and habitats within the forest canopy) are separately monopolized, 2) uniquely exploiting plants, both in part and whole (i.e., fruit pulp, flesh seeds and/or skins,etc.) in various stages of growth cycle, and 3) varying food choices or "preferred" items. In addition, responses may include alternations relating to the times chosen for food allocation and the means by which such food is acquired.

In relation to hominoid evolution, a certain degree of niche differentiation invariably existed among competing ape and monkey species. Indeed, today observations of extant hominoids confirm that they are not able to exclusively exploit their local habitats. Rather, in most instances, apes must compete for shared resources with sympatric primate species. For African apes of the early to middle Miocene, resource availability, while it invariably became increasingly restricted, would likely not have been of such spatial and temporal scarcity as to promote extreme levels of competition with sympatric monkeys. Elaborating upon Clutton-Brock's ideas (1977), it might be logically inferred that under conditions of low competition, early mid Miocene hominoids and cercopithecoids might have still been able to exploit the same general resource base, but with an differential focus in relation to how, when and which resources to consume. As Napier (1969) was the first to develop, variations in diet and locomotion would have afforded a certain degree of sympatry among evolving apes and monkeys during the Miocene insofar as they would have allowed for such differential exploitation of similar/shared resources. Such adaptations are of tremendous import to the survival and ultimate evolution of primates for, as Napier aptly explains "...locomotion and diet are so intimately related that it is hardly meaningful to give one or the other an adaptive priority ; (all) animals must move to eat and eat to move" (Napier 1969, p.79).

Publications subsequent to Napier's, further advanced an understanding that adaptations relating to locomotion, as well as food acquisition and consumption/digestion, would have afforded Miocene hominoids a limited success in spite of potential conflict and competition with cercopithecoids (Temerin and Cant 1983; Andrews 1985a). The ability for these Miocene primates to coexist under conditions of minimal intra-specific competition would have been strongly moderated by the amount of stress internal to the ecosystem of which they were part. As the stress of resource depletion and environmental desiccation continued through out the middle Miocene, competition would have invariably risen to levels precluding any degree of sympatry.

Niche Exclusion: The next logical response to ecological stress after the limits of niche differentiation have been exceeded would be complete niche exclusion. The progressive fragmentation of the early Miocene African tropical forest biome into a "patchwork of microhabitats", each able to sustain fewer and fewer species, would have been a primary impetus to the outward migrations of specific groups from their "natal" niche to dispersed islands of resources (Malone 1987). The outward migration of hominoids, although it would be effected by dietary adaptations, would have likely been better facilitated by physical and, to a lesser extent, social adaptations (Andrews 1985a). Indeed, dental evidence does suggest a definite trend of middle Miocene apes away from the strictly frugivorous diet previously shared with early Miocene monkeys (Andrews and Martin 1991; Andrews 1985a; Kay 1984). However, locomotor strategies would have been of more definite advantage insofar as they would have contributed to a greater efficiency in the allocation and exploitation of small and/or spatially discrete food patches (Andrews 1985a; Temerin and Cant 1983).

Competition with coeval monkeys would have provided a definite impetus for the niche exclusion and subsequent migration of Miocene hominoids. During the early stages of the middle Miocene, the overall diversity and distribution of apes within the Old World

greatly increased (Andrews 1985a). In Africa specifically, however, the relative diversity of the apes began to decline significantly into the middle Miocene - such as would be expected for increasingly eurytypic populations. However, as Andrews (1985a) would contend, while diversity declined within Africa, the number of ape species relative to monkey species, was to become significantly greater *outside* of Africa during this same time period. Such a trend provides great insight not only into patterns of niche exclusion and their relevance to hominoid evolution, but also into the evolutionary benefits conferred to migratory patterns and processes.

Adaptations to Stress and Competition

As the discussion above suggests, the way in which primates respond to changes in the ecosystem (i.e., extinction, niche differentiation, and niche exclusion) ultimately can be moderated by any variety of adaptive abilities. This section will discuss the various behavioural and morphological adaptations, observed or inferred, that may have contributed to the responses and ultimate survival of the competing Miocene apes and monkeys.

Behaviour: As Temerin and Cant (1983) explain, food acquisition is a fundamental determinant of a primate's adaptive strategy. Evidence supports the idea that feeding among all primate groups is not a random activity, but rather one guided by definite preferences for certain food (Milton 1984, 1993). On the whole, the primate order is strongly dependent on plant foods (Milton 1984). However, the kinds and quantities of plants consumed by primates are not intra-specifically uniform. Rather, food exploitation can range from complete insectivory, to complete folivory, to complete frugivory and ultimately to any combinations of each or all food preferences (Kay 1984). In nature, the most energy and nutrient rich food items (i.e., protein and carbohydrate)

available to primates are insects and animal flesh. However, the exclusive exploitation of insects is limited among primates. More specifically, factors of insect size combined with the obvious difficulties involved with the access and availability of insects over time and space, render insects a very energy-inefficient food source. As will be developed in more detail later, small food items such as insects are of limited caloric/energetic value to medium to large sized primates (Kay 1984). As with insects, the acquisition and exploitation of animal flesh is similarly rare insofar as the energy spent on the allocation and acquisition (i.e., the hunting down process) of such high-energy protein sources is great and not always compensated through consumption. Frugivory, or the heavy reliance of fruits and nuts, is a more frequent diet type among primates. As Kay (1984) develops, such a diet relies heavily on food items containing fewer carbohydrates and proteins . Consequently, the ability to subsist on an entirely frugivorous diet requires that large spatially and temporally consistent resources patches are available. Folivory, or a diet based on the consumption of leaves, stems, shoots and buds, has the potential of providing great quantities of both carbohydrates and proteins. However, Kay (1984) maintains that such a potential is reached only when large quantities of leafy items are consumed. Because of the restrictions posed by each of the above dietary regimes, it is often essential that primates, in order to survive, maintain a balanced diet supplemented by of all the above resource groups.

While certain foods may be preferred by some primates, the fact is that limitations posed by variability in food abundance, food quality and the inherent physical/metabolic characteristics of certain food stuffs ultimately determine which foods can be/are exploited (Milton 1984). As Milton (1984, pp. 250-256) explains, as primates adapt and evolve, so too do plants. Plants can become of less utility to their primate consumers insofar as: 1) they tend to make themselves less accessible over time and space, and 2) they can acquire mechanical (i.e., hard outer shells, needles, thorns, hairs) and chemical deterrents.

Ultimately, the extent to which primates are able to meet their energy requirements, in light of the obvious potential for variation in plant numbers, kinds and quality, depends on the physical/morphological attributes they possess/acquire which allow for these primates to overcome energetic restrictions.

The ability and overall efficiency of a primate to access and consume their preferred foods is directly linked to a repertoire of adopted behaviours (Temerin and Cant 1983; Cant and Temerin 1984; Oates 1987; Clutton-Brock 1977). Certain behaviours, embodying capacities of sociality, cognition, perception, and travel, all contribute to foraging efficiency (Cant and Temerin 1984). When to forage, how to locate food patches, which food patches to exploit, how to most efficiently move within/between food patches, how to acquire, prepare and digest food items, how long to exploit a food patch and how to defend a food patch or a series of patches are just some of the problems that can be encountered by primate groups/individuals and which can , in turn, be overcome through specific behavioural capacities (Cant and Temerin 1984; Oats 1987). For all primates, the optimum result of adaptive foraging behaviours is achieved when the gross energy gain is greater than energy (and time) expended in allocating, preparing and consuming/digesting these food items (Temerin and Cant 1983, pp. 336-337; Pyke *et al.* 1977).

Morphology: Of course, it is impossible to directly observe behavioural capacities from the primate fossil records. What can be known about behavioural capacities can be inferred from any number of physical/morphological clues left behind. Fossil remains provide not only a direct view into the past, but also a stable base of factual evidence from which more intangible aspects of adaptation can be conjectured. Of importance to understanding morphology, and hence possibly behaviour, is realizing how living primate species may serve as analogous representatives (both behaviourally and morphologically) of their ancestors (Kay 1984, p. 22).

i) Body size and metabolism: Overall indications of body size, which *are* directly measurable or which are, at the very least, easily estimated, can be used to reveal definite clues about foraging behaviours among extinct primates (Kay 1984; Temerin *et al.* 1984). According to the Jarman-Bell principle, a small animal is able to subsist on small, but energy rich resources, such as insects (Jarman 1974; Bell 1971; Kay 1984). While the metabolic rates of smaller animals tend to be quite high (per gram of body tissue), energy requirements can easily be met through the consumption of smaller quantities of food, provided that each of these foods contains a higher potential of unit energy . Further,as the absolute size of an animal increases, so too do its absolute resource intake requirements. While *larger quantities* of food are required by larger animals, these foods can be of *less energetic value* in relation to the body weight of the individual (Jarman 1974; Bell 1971; Kay 1984; Conroy 1990, pp. 32-34). As Kay devises (1984), a series of weight thresholds can be established by which the kinds and degrees of primate resource exploitation can be determined. In relation to correlations between body size, metabolism and foraging behaviours, Kay (1984, p. 29) concludes that:

> All of this has an important application to the study of extinct primates. Animals that achieved an adult body weight of greater than 350g could not have been primarily insectivorous, meaning that no more than 30% to 40% of their energy needs could be filled by insect-eating. By the time 1 kg is reached, this percentage would be much less. At small size, an animal supplementing its insectivorous diet with leaves would compound its difficulties; below about 700g body weight, folivory is difficult to sustain energetically. We should expect to find extinct folivores only at or above 700g body weight.

Among both extant and extinct higher primates (including cercopithecids and hominoids) the average species' weights far exceed 350 g, which essentially means that these primates cannot/could not have sustained themselves on a purely insectivorous diet (see Fleagle and Kay 1985). In fact, the great majority (if not the entirety) of higher catarrhine primates are above the 700 g threshold. As a result, while most primates (even

those of larger body size) do maintain a heavy reliance/preference for fruits, their absolute body size will tend to necessitate that any frugivorous diet be supplemented with the energy, proteins and/or bulk made available through alternate food sources (i.e., insects, animal flesh and/or leaves, etc.) (Kay 1984). The reliance of all higher primates on the same general resource base can be of direct consequence in regards to the degrees of intra-specific competition experienced. Indeed, this would be of double consequence during times of extreme environmental/resource stress. Consequently, other morphological characteristics must have come into play over the course of Miocene ape evolution if these hominoids were successfully to compete with coeval monkeys.

ii) Teeth: Dental adaptations are key to understanding primate diets and foraging behaviours. In regards to palaeoprimatological reconstruction, teeth are of tremendous import given their abundance in the fossil records. As Kay (1984) explains, the shape and configuration of teeth vary in accordance to their conferred function. For example, Kay develops that among Old World anthropoids, there is a noted relationship between incisor size and food handling. In general, Kay explains that larger and more broad (i.e., mesially-distally) incisors tend to suggest a greater reliance on "incisal preparation" and general access to certain food sources (i.e., biting though thick outer shells, skins, bark, etc.). Molars function in the relation to the chewing, grinding and early digestion of food (Kay 1984, pp. 31, 43). At a more specific level, the molar crowns of folivorous primates, such as modern cercopithecoids, serve as shearing and cutting devises for the break-down of tough, fibrous foods such as leaves. In fact, Kay maintains that sharp shearing blades are thought to facilitate the break-down of tough, complex carbohydrates early in the initial stages of the digestive cycle. As such, molars belonging to folivores demonstrate cusps (bi-lophodont) of high relief with sharp apices. Generally, thin enamel is associated with a folivorous diet. As Kay (1984, p. 37) explains, thin enamel is easily worn down through dental wear. Consequently, with continued dental wear enamel

prisms or windows become exposed along the cusp margins and these, in turn, produce sharper edges better suited to masticatory shredding and slicing. Such dental trends are generally associated with the evolution of cercopithecoid primates. However such dental features may not have become fully manifest until the latter stages of the Miocene (McCrossin and Benefit 1994).

In contrast to the above, low molar relief and thick enamel indicates a diet reliant on hard and difficult to open food items such as nuts and hard, thick-skinned fruits. As Kay (1984, p. 38) explains, "...(it can be assumed) that the thick enameled extinct species were *not* efficient consumers of leaves or other high-fiber foods". The low relief of these teeth provides a greater surface area which accommodates the greater occlusal forces necessary for crushing foods. In essence, thick enamel helps to prevent unnecessary wearing of the teeth (i.e., the exposure of enamel prisms and sharp edges are of little adaptive significance to such). During the course of primate evolution, specifically hominoid evolution, the development of a large, thick enamelled molar has generally been attributed to a growing tendency towards a more varied diet (i.e., not one reliant on exclusively ripe fruits or leaves), and possibly, the subsequent trend towards an increased reliance (but *not* exclusive reliance) on a terrestrial way of life (Andrews and Martin 1991).

iii) Gut morphology: In moving down the digestive tract, the next morphological features of relevance to primate feeding adaptations are those of the stomach and intestines. Of course, such soft tissue features do not preserve in the fossil records. However, how certain gut features serve to the adaptive advantage of extant primates can provide us with some insights as to how these same features may have evolved and functioned among extinct primates.

As Milton (1984) develops, many food stuffs exploited by extant primates hold very little nutritive value. The problems of low nutritional contents can, in some instances,

be confounded by high levels of indigestible materials and chemicals, some poisonous, within the resources consumed. Among cercopithecoid monkeys, these problems have been overcome through different morphological adaptations in the gut (Napier 1969; Andrews 1985a; Milton 1984). As mentioned, molar-cresting among cercopithecoids helps in the early digestion of plant materials, a digestion which is likely further accelerated by the presence of quantities of digestive enzymes in saliva (Andrews 1985a). Cercopithecine monkeys demonstrate a certain gastro-intestinal tolerance of unripe, possibly toxic, fruits. Bacterial and protozoan activity in the highly acidic, sacculated stomach of these monkeys allows for a certain degree of detoxification to take place (Andrews 1985a). Colobine monkeys have similar sacculated stomachs. In contrast however, it appears that the stomachs, small intestine and caecums of the colobines are much more complex in their internal micro-floral and chemical constitution which allow for the digestion of otherwise poisonous and indigestible food items (Andrews 1985a).

Hominoids appear to have very few gut adaptations when compared to their monkey counterparts (Andrews 1985a). However, there is evidence which suggests that a prolonged transit time through the digestive tract might help to increase the amounts of foods digested and absorbed into the body (Milton 1984). As Milton further develops, any low quality foods consumed will pass through the system more slowly, while more nutrient-rich foods will pass more quickly. Among great apes and humans, the transit of food among *Pan* and *Homo* appears to be much quicker than that of *Gorilla* and *Pongo*. This discrepancy Milton attributes to the general trend of the former two genera towards the exploitations of higher quality resources - a trend which she further explains "...was retained and intensified during hominid evolution in a savanna-mosaic setting and is still characteristic of the hominid line today" (Milton 1984, p. 269).

iv) Post-cranial morphology: Post cranial evidence can provide some clues into the locomotor and postural adaptations acquired by evolving primate lines (Ripley 1979;

Temerin and Cant 1983; Andrews 1985a; Malone 1987). Brachial (BI = length of radius/length of humerus x 100), crural (CI = tibial length/femoral length x 100) and intermembral (II = length of radius & humerus/length of femur and tibia x 100) indices can be employed to predict certain locomotor tendencies among primates (Conroy 1990, p. 76). Generally four patterns can be determined using each of these indices. Often, the intermembral proves to be the most usful. The intermembral index identifies four locomotor types, these are: 1) general arboreal quadrupedalism, as distinguished by forelimb length approximating hind limb length (II = ~100), 2) arboreal leaping/climbing, wherein the forelimbs are slightly longer than the hindquarters (II = < 100), 3) suspensory or brachiating locomotion, as indicated by forelimbs significantly longer than hind limbs (II > 100), and 4) terrestrial quadrupedalism, where the hind limb proportions dominate for limb proportions (II = ~ 100) (Conroy, p. 77).

To varying degrees, each means of locomotion has come into play over the course of primate evolution. More specifically, and in relation to Miocene catarrhine evolution, the trend among hominids has been away from a primitive catarrhine quadrupedalism towards a more diverse array of locomotor adaptation (Malone 1987). While Old World monkeys have for the most part maintained a heavy reliance on quadrupedalism (terrestrial and arboreal), hominoids have adopted a more eclectic approach to locomotion (Andrews 1985a; Temerin and Cant 1983). As Temerin and Cant (1983) explain, the quadrupedal abilities of cercopithcoids have allowed them to maintain a monopoly over their resource domain of leaves and unripe fruits. In evolutionary terms, Old World monkeys did not adapt to environmental stress through postcranial changes and locomotor differentiation, but rather adapted through dietary means (i.e., exploiting increased amount of leaves and unripe fruits in lieu of ripe fruits) (Temerin and Cant 1983). By contrast, it has been suggested that evolving hominoids developed a new and diverse suite of locomotor behaviours. Within the confines of the forest, terminal branch feeding by means of slow,

quadrumanous, suspensory locomotion, would have come about as a means of allowing apes to effectively exploit resources unaccessible to competing monkeys (i.e., ripe fruit) (Malone 1987). As Malone (1987) concludes, under the influences of ever-increasing environmental stress and the subsequent depletion of resources, a semi-arboreal or terrestrial form of locomotion would have allowed for these apes to efficiently travel and forage between any number of spatially discrete resource patches.

Evolutionary Consequences of Adaptation

While ideas as to when, how and why a divergence in primate locomotor and other adaptive patterns and processes took place during the Miocene remain for the most part unclear, even our vaguest understanding of such circumstances is of the utmost importance in determining the spatial and temporal displacement and evolution of hominoids and humans. As this discussion has explored, factors of environmental stress and resource competition have variably influenced extinctions or, conversely, continued survival (through adaptation) of Miocene primates. At most, under conditions of *minor* environmental stress during the early and middle Miocene of Africa, adaptation and subsequent evolution among primate groups likely resulted in varying degrees of niche differentiation. However, more severe, competitive ecological circumstances would invariably have contributed to a greater expression of adaptive diversity among evolving catarrhines, both hominoid and cercopithecoid. Extensive geographic expansion and partitioning of groups would have initially resulted in a marked increase of species divergence through allopatric speciation (Foley 1991). Such speciation would have been of the greatest impact for the more stenotypic cercopithecoids, whose adaptive response would have been extreme (i.e., exclusion and biological/morphological specializations). In contrast, however, as hominoid species expanded their geographical range and adapted

to the limitations of resource depletion through eclectic behaviours and generalized morphologies, their rates of speciation would have declined (Foley 1991, p. 425).

During the Miocene, the overall representation (both in kinds and numbers) of apes in the fossil records underwent a serious decline, specifically in Africa, but this decline might be an artefact of regional sampling bias (see Chapter Four section on taphonomic bias). Global evidence documenting the successful adaptions of hominoids migrating into Eurasia should attest to the fact that these hominoids were far from being "evolutionary failures" (Andrews 1985a, p. 25). Repeated fluxes in climate and resource stress throughout the Miocene would have been readily countered by a repertoire of eurytopic adaptations and characteristics (behavioural and morphological) possessed by these hominoids. As demonstrated, such adaptations would have ensured success and hominoid survival within early Miocene Africa . Still further, modes of adaptation and evolution would have facilitated a varied and rich life *outside* of Africa, in Eurasia. Finally, under the influence of a new suite of ecological conditions and constraints within Eurasia, the close of the Miocene would have set the stage for new episodes of adaptation, evolution and, possibly, an eventual re-invasion of large bodied hominoids into Africa. The next chapter of this thesis will look in more detail at the cast of Miocene primate characters with specific emphasis given to their palaeoecological context and morophological variations. Ultimately, it will be demonstrated how the dynamic relationships between these diverse catarrhine groups, both ape and monkey, and their conceived/inferred adaptations facilitated the emergence, survival and evolution of hominoids in both Africa and Eurasia.

Chapter Three

The Cast of Players: A Review of the Fossil Evidence

Fundamental to a clear understanding of the process of hominoid evolution is a comprehensive and complete reference base. Of course, the nature of the fossil record is such that this sort of reference base is difficult, if not impossible, to assemble. Geographically speaking, it is estimated that less than .1% of the African continent, principally east Africa, has been sampled for fossil primates (Hill 1994). Consequently, it can be deduced that from this .1% only a very small fraction of *all* possible exinct primates have been uncovered. These figures appear even smaller when it is taken into consideration just how vast the areas beyond the confines of east Africa are and, in turn, just how *few* of these areas have actually been sampled for their fossil potential.

In spite of this obvious deficit of palaeoanthropological evidence, all those fossil that to date have been recovered, can and do provide valuable clues into the pattern and process of hominoid development. This chapter will provide an overview of that fossil evidence which best documents catarrhine primate evolution throughout the Miocene of the Old World. First, a review of the phylogenetic relationships of catarrhines, as distinct from other anthropoids, will be conducted. Using the primitive anthropoid and catarrhine morphotypes as a comparative starting point, the phylogenetic relationships and defining characteristics (ancestral morphotypes) of cercopithecoids, hominoids and hominids will be outlined. Next, a more detailed study of the Miocene catarrhine fossil record will be conducted. Wherever possible, aspects of the palaeoecology and specific morphologies and adaptations (i.e., behaviour as indicated through cranio-dental and post-cranial evidence) will be outlined. The end result of such a study will be the establishment of an adequate reference base upon which reconstructions of cercopithecoid - hominoid dynamics and the subsequent evolution of hominoids can be founded.

Establishing Ancestry and Phylogeny

In order to understand how hominoids and cercopithecoids have evolved, it is essential to first understand from whence they came, i.e., from what ancestral stock they were born of and from which they diverged/derived. Of key importance to defining primate morphotypes as distinct and discrete is the recognition of apomorphic features, as these shared features are the prerequisites for any definitions that might be constructed for all Old World Primates (Andrews 1985b). Figure 6 provides a basic phylogenetic reconstruction, as based on apomorphic chararacteristics, of the various ancestral morphotypes which are often used to define all catarrhines. Appendix A provides a more comprehensive listing of the apomorphies defining each node.

Ancestral Anthropoid Morphotype - Node One:

All extant monkeys, both Old World and New World, and apes belong within the primate suborder Anthropoidea. While the suborder as a whole does retain some characteristics of a more primitive ancestral morphotype (i.e., such as those shared with Prosimians and Tarsiiformes), it is important to recognise those traits which are *unique* to this suborder - namely those *synapomorphic characteristics* which *distinguish* this suborder from all other primate groupings (For a complete listing of both primitive and derived anthropoid traits consult Harrison, 1987). In general, extant anthropoids are identified by such observed features as short faces, dry rhinarium, reduced facial whiskers, small immobile ears, forward placed eye-sockets evidencing diurnality, the replacement of claws by flat nails, and an apparently non-specialized anterior-dentition (i.e., no toothcomb) (Napier 1986). Of course, not all these features are readily observable, through lack of preservation, in the fossil records. However, Harrison (1987) maintains

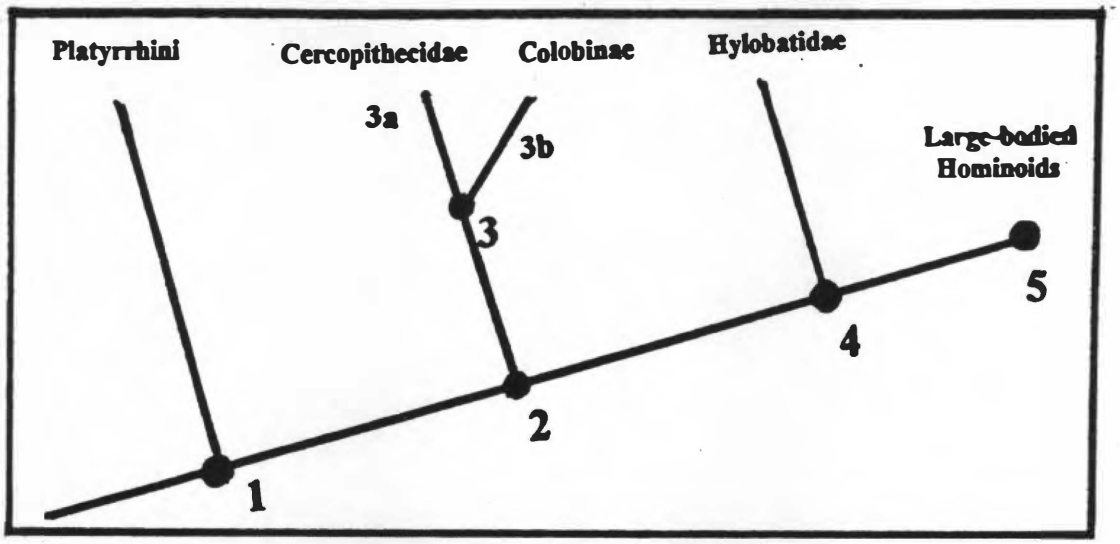


Figure 6. Phylogenetic Reconstruction of Catarrhine Primates.

that there are at least 15 derived features unique to Anthropoidea, especially those relating to cranio-facial, dental and post-cranial evidence, that can readily be used to identify fossils belonging within this suborder (Appendix A, Node One).

Eu-Catarrhine Morphotype - Node Two:

Within the Anthropoidea suborder there exist two distinct primate infra-orders: 1) Platyrrhini and 2) Catarrhini. Each infraorder, to varying degrees, retains features primitive to the Anthropoidea as a whole (Szalay and Delson 1979; Andrews 1985b; Napier 1986; Harrison 1987). Of importance to this discussion is not which primitive features were supposedly primitive retentions within these infraorders, but more specifically which features became those which best differentiated the two as separate and distinct primate groupings. With regards to the Catarrhini, or all Old World Monkeys and Apes, the ancestral morphotype shared by all extant and extinct eucatarrhines is defined by an extensive suite of derived characteristics (Szalay and Delson 1979; Andrews 1985b; Harrison 1987). The principal, defining features derived and unique to the Catarrhines

include cranio-dental transformations such as: 1) the development of tubular ectotympanic of the auditory regions, 2) complete post-orbital closure as marked by a disappearance of the lateral orbital fissure, 3) the loss of the second premolar and the subsequent reduction in the dental formula to 2-1-2-3, 4) occlusion of the upper canines with the lower third premolars, and 5) an overall modification of the molar teeth (Szalay and Delson 1979; Harrison 1987). Postcranial features of the the shared eucatarrhine morphotype include modifications of the forelimbs (i.e., absence of the entepicondylar foramen and the appearance of a deep olecranon fossa on the humerus, to name just two) and of the hindlimbs (i.e., a lengthening of the talus, and modifications in the hallical joint with an absence of a prehallux) (Andrew 1985b; Harrison 1987). Node Two (Appendix A) outlines the phylogenetic placement and defining characteristics of this Catarrhine infraorder.

Morphotypes within the Cercopithecoidea - Node Three:

Cercopithecoidea today is the largest, most diverse superfamily among Old World catarrhines. At a very generalized level, extant Old World monkeys are readily distinguished from platyrrhines by their down-turned nasal openings and are further distinguished from not only platyrrhines, but also hominoids, by their distinctive ischial callosities (Napier 1986). On the whole, cercopithecoids do tend to express an overall uniformity in their morphological repertoire when compared to other anthropoid taxa (i.e., platyrrhines, and hominoids). This is because they appear to have acquired fewer specializations over the course of evolution (Schultz 1969). However, fossil evidence does demonstrate that all taxa within cercopithecoidea do share a unique suite of cranial, dental and morphological features which do definitely separate this superfamily the Hominoidea morphotype. Dentally, one of the most distinguishing features of the cercopithecoids is this superfamily's loss of the hypoconculid on the molar teeth (Delson

1975; Andrews 1985b; Strasser and Delson 1987; Harrison 1987). Essentially, this loss of the hypoconculid, combined with an overall elongation of the cheek teeth, has resulted in the formation of a bilophodont dentition (Strasser and Delson 1987). Unique canine orientations and morphologies also separate the cercopithecids from the earlier, more primitive catarrhines, as well as from the more derived hominoid condition. Postcranial modifications involving the elbow, wrist, hip, ankle and foot joints, such as those which likely provided joint stability and mobility in quadrupedal locomotion, are also distinguishing features of Cercopithecoidea (Strasser and Delson 1987; Harrison 1987).

Within the Cercopithecoidea superfamily, there exist two major subfamilies: 1) the Cercopithecines (Node 3-A), to which the tribes Papionini (extant macaques, baboons, drills, mangabeys and gelada) and Cercopithcini (forest guenons and relatives) belong, and 2) the Colobinae (Node 3-B), to which the Asian and Africa subtribes of colobus monkeys belong (Strasser and Delson 1987). Morphologically, these two subfamilies express very unique morphotypes (consult Appendix A). In sum, and as Strasser and Delson (1987) explain, the great majority of characteristics, which distinguish these primates from not only from the ancestral morphotype but also from each other, are uniformly associated with dietary adaptations and specializations. Postcranial modifications in colobines, such as those associated with the adept arboreal running and leaping of these monkeys, further help to distinguish between the two subfamily divisions within Cercopithecoidea (Strasser and Delson 1987).

Hominoidea Morphotype- Node Four:

Hominoidea is the second, and only other major superfamily distinction among the Catarrhini. The sum of this superfamily consists of all hylobatids (lesser apes), great apes (African and Asian) and humans. As a whole, this superfamily is readily defined by an extensive suite of apomorhic characteristics (Appendix A)(Harrison1987; Andrews

1985b). Postcranially, these characteristics are said to contribute to discrete functional complexes each of which is associated with distinct locomotor and positional behaviours. Such complexes relate to: 1) the increased ability to rotate the forearm, 2) the increased ability to extend the arm at the elbow, 3) the ability to elevate the arm above the head, 4) an overall tendency towards forelimb dominance in relation to locomotion and feeding, 5) a greater flexibility of the wrist and opposable thumb, 6) the tendency towards more erect posture in conjunction with both locomotor and positional behaviours, and 7) more mobile ankle and hip joints (Harrison 1987; Andrews 1992a). Craniodentally, hominoids are thought to express more primitive, generalized features reminiscent of the ancestral catarrhine morphotype (Harrison 1987; Andrews 1992a). However, while such features might be seen as ancestral to catarrhines, they might also be viewed as unique dietary adaptations (homoplasies) that have independently evolved (Andrews 1992a).

Ancestral Morphotype of Large Bodied Hominoids - Node Five:

Among hominoids, after the exclusion of Hylobatids, there exists a distinct ancestral morphotype which may be used to define all of the African and Asian great apes, humans, and each of these large bodied hominoids' putative ancestors. (Andrews 1985b; Kay 1986; Martin 1986; Andrews 1992a; Begun 1992b). A more extensive listing of the key derived traits for this morphotype is found in Appendix A. Defining characteristics of this clade include both cranio-dental and postcranial changes. Dentally, there are a number of features unique to this group, not the least of which is the overall, marked change in the shape/configuration of the incisors and premolars, coupled with an increase in size relative to the molars (Andrews 1992a; Begun 1992b). As viewed in Appendix A, unique features in the postcrania are predominantly linked to changes in the forelimb and are attributed to an increased tendency towards forelimb dominated suspensory locomotion (Andrew 1985b).

In relation to all those species (extinct and extant) belonging to this morphotype, there exists great debate as to the degree to which each of these species may (or may not) be related to one another vis a vis certain shared, derived features. The general consensus holds that the large bodied Asian ape forms a clade separate from all other large bodied apes (Andrews 1985b; Martin 1986). However, it is from among the remaining hominoid groups (African apes and humans) that the greatest amount of confusion and debate has arisen. Essentially, there are currently three main views regarding relatedness among all large bodied, non-Asian hominoids. The first group contends that a trichotomous relationship links all African apes and humans into one distinct grouping, to the exclusion of Asian apes (Andrews 1992a). However, much of this information is based almost exclusively on molecular/genetic information as opposed to fossil/morphological evidence (Ward and Pilbeam 1983; Andrews 1986; Andrews and Martin 1987; Andrews 1992a). Some research indicates that such molecular evidence is flawed with "technical and philosophical issues which cast doubt on the usefulness of most of this evidence in phylogenetic inferences" (Kluge 1983, p. 158). In addition, very recent fossil discoveries are beginning to show just how very "out-of-sync" the clocks of molecular and morphological evolution can be (as cited by Gibbons and Culotta 1997) and, consequently, how molecular notions of phylogenetic relatedness may be skewed and, to an extent, unreliable. In contrast to the above, a second group feels that morphological evidence supports a unique morphotype shared only between *Pan* and humans and their putative ancestors, to the exclusion of *Gorilla* (Begun 1992b). Still another group maintains that all African apes form a distinct sister group to all Plio-Pleistocene hominines (i.e., Homininae) (DeBonis and Koufos 1997).

Of course, since the final word in such an on-going debate will only ever be had when it is discovered how to determine with 100% accuracy instances of apomorphic, plesiomorphic and homoplastic similarity among fossil hominoids, it is unlikely that a point

resolve will ever be reached. Indeed, depending on the functional/adaptive importance given to one trait (or a complex of traits) over another, there is some personal bias involved in distinguishing those features which are truly shared or, conversely, which are parallelisms. It is not the aim of this thesis to alleviate such bias or to solve the underlying problems. By contrast, the aim is to simply reveal these traits (whether homoplastic or not) and to show their adaptive significance in an immediate/ecologically based setting and not exclusively in an evolutionary and/or phylogenetic context. While a tremendous amount of variability may be said to exist among all fossil hominoids (especially large bodied African apes and humans) the general consensus maintains that these same hominiods are all very closely related (see Begun 1995). Given the increasing variability observed among hominoids, it might be best to simply view morphological trends and discrepancies as evidence of an increasing eclecticism and plasticity among these higher primates - even if this means distancing palaeoanthropological endeavors from parsimonious analysis and espousing the notion that homoplasy (i.e., hominoid plasticity) may, in fact, be more common place than is typically thought.

Fossil Apes and Monkeys

The origin, both temporal and spatial, of hominoids and cercopithecoids is very uncertain. However, it is probable that the first semblance of a "catarrhine" morphotype preceded true catarrhines by at least ten to fifteen million years (Fleagle and Kay 1985; Fleagle 1986). The earliest, most primitive catarrhine forms *may* be traced back to the Jebel Qatrani Formation of the Oligocene (~31 Ma)(Andrews 1985b; Fleagle and Kay 1985; Fleagle 1986; Harrison 1987). Such early "catarrhines" may be represented in the fossil remains of Parapithecoidea and the genera *Aegyptopithecus* and *Propliopithecus* (Harrison 1987). However, any semblance of these primitive primates to the derived

catarrhine condition is clouded by a tremendous number of retained primitive characteristics. In fact, certain cranial and post-cranial elements hint that these primates were likely not all that far displaced from platyrrhine monkeys, and therefore were not probable ancestors to later, true catarrhines (Andrews 1985b; Fleagle and Kay 1985; Fleagle 1986; Harrison 1987).

The earliest undisputed catarrhines likely did not appear until the beginnings of the early Miocene of East Africa. However, recent catarrhine finds do suggest that the first appearance of true catarrhines, perhaps even true hominoids, may have extended as far back as the terminal Oligocene of east Africa (Leakey *et al*. 1995a). The next section will provide an overview of the *key* fossil catarrhines, both hominoid and cercopithecoid, as they appeared in late Oligocene and throughout the Miocene of Africa and Eurasia. What follows is *not* a comprehensive discussion of *all* fossil catarrhines, but rather it is a selection of the more relevant, best understood taxa. The discussion of each taxon will, whenever possible, cover aspects of palaeoecology and morphology (i.e., dentition, body size, and post-cranial morphologies). Palaeoenvironments and morphology are extremely revealing and helpful in the reconstruction of primate behaviours and adaptations within their ecosystems.

Latest Oligocene - African Hominoids (~27-24 Ma):

***Kamoyapithecus*:** Recent discoveries of this large bodied primate at the Lothidok Range Site in northwestern Kenya are said to represent one of the earliest hominoid forms in east Africa (Leakey *et al.* 1995a). No detailed studies of this primates' palaeoenvironment are yet available. However, given the high global temperature at this time (refer back to Figures 5a and b) and an absence of regional rifting, the conditions would have been extremely favorable for a very lush, warm, tropical forest setting. The only evidence uncovered for this new species is dental. While some primitive catarrhine

characteristics are apparent in these finds, others appear to demonstrate a more derived condition. *Kamoyapithecus* appears to share certain molar (including low reliefed, thinly enamelled molars) and premolar configurations with early Miocene hominoids, such as *Proconsul* (Leakey *et al.* 1995a). Aspects of the anterior dentition (i.e., breadth and depth of the incisors) appear also to link this hominoid closely with later Afropithecines (Leakey *et al.* 1995a). In sum, all aspects of the dentition demonstrate that this hominoid was likely a frugivore whose dietary regime produced some anterior tooth stress (i.e., anteriorly), but with only minimal degrees of attrition on the posterior bunodont molars (Leakey *et al.* 1995a).

Early Miocene - African Hominoids (23-16 Ma):

***Proconsulidae*:** This family of early Miocene primates provides clear evidence of early "hominoid" diversity. There may be as many as six different genera attributed to this family, which include *Dendropithecus*, *Proconsul*, *Rangwapithecus*, *Limnopithecus*, *Micropithecus* and *Simiolus* (Fleagle 1986, 1988). While the diversity of these early "hominoids" was tremendous, their known geographic range, as restricted to sites in Kenya and Uganda, was small.

i) *Dendropithecus* (20-17Ma): This genus is believed to have lived in tropical forest and woodland areas (Andrews 1992a). However, new evidence indicates that these primates likely existed in semi-dry upland forests (Retallack *et al.* 1995). In terms of proconsulid affinities to all hominoids, great debate surrounds the phylogenetic placement of this early Miocene proconsulid genus. Such debates stem from the mosaic of features, both primitive and derived, which have been used to link it to: 1) the primitive catarrhine morphotype, 2) the hylobatid morphotype, and 3) a morphotype most similar to coeval Miocene primates (i.e., *Proconsul*) as well as true hominoids (Harrison 1987). The average body size of this genus is estimated to have been around 9 kg (Rose 1994; 1997).

Postcranial elements of the forelimbs seem to suggest that this primate was very likely a long-limbed quadruped. While these primates were predominantly quadrupedal movers, evidence from the hindlimb appears to indicate that these modes of locomotion were interspersed with high occurrences of suspensory and climbing behaviours using all four limbs (Rose 1994; 1997). Dentally, *Dendropithecus* retained many features of the primitive catarrhine morphotype (Harrison 1987). Some evidence suggests that teeth were likely used for food preparation in a diet based almost exclusively on fruits (Fleagle and Kay 1985).

ii) *Proconsul* (22-17Ma): With hundreds of specimens representing this genus already collected, a great deal is known about *Proconsul*. Four *Proconsul* species are currently recognized: *P. major*, *P. africanus*, *P. nyanzae* and *P. heseloni* (Ward *et al.* 1993; Walker *et al.* 1993; Retallack *et al.* 1995; Walker 1997). While viewed as a primitive catarrhine in many respects, certain derived features appear make it a close ancestor to all great apes and humans (Harrison 1987; Retallack *et al.* 1995; Walker 1997). Generally, species of this genus are thought to have lived in predominantly forested and woodland tropical regions (Pickford 1987b; Andrews 1992b; Andrews *et al.* 1997). However, recent analyses demonstrate that there was a tremendous amount of diversity in the palaeoenvironments and niches exploited by these hominoids, with greatest evidence supporting "... woodland with patches of dry forest, open early successional vegetation and local grassy woodland ..." (Retallack *et al.* 1995, p. 84). The range in body-size for these primates was great, with the smallest (*P. heseloni*) approaching the size of a siamang and the largest (*P. major*) the size of a female mountain gorilla (Walker 1997). Postcranial remains strongly support that all *Proconsul* species were slow and deliberate quadrupedal arborealists none of which practiced any form of suspensory, leaping or climbing locomotion (Rose 1994; Walker 1997). Dental evidence, including observations of tooth shape, the length of shearing crests and microwear, all seems to

confer that all proconsulids were frugivores (Walker 1997). Evidence of relatively thin molar enamel also corroborates this notion of a frugivorous diet (Andrews and Martin 1991).

iii-vi) *Micropithecus, Limnopithecus, Rangwapithecus* and *Simiolus*: All these early Miocene hominoids are poorly understood (McCrossin and Benefit 1994). With the exception of *Rangwapithecus*, all these primates are considered "small-bodied apes". Available dental and postcranial evidence suggests that these hominoids represent a mosaic of adaptations (Rose 1997; Kay and Unger 1997). Tooth evidence, especially that relating to molar cresting, suggests that both *Limnopithecus* and *Micropithecus* had low rounded cusps such as those best suited to a frugivorous diet (Leakey and Leakey 1987; Kay and Unger 1997). By contrast, *Simiolus* and *Rangwapithecus* demonstrate relatively high crowned, sharply crested teeth. These features indicate that these apes had greater folivorous components in their diets (Leakey and Leakey 1987; Andrews and Martin 1991; Kay and Unger 1997). Benefit and McCrossin (1995) attribute the increased tendency of such hominoids towards folivory to the persistence of these species into the later stages of the early Miocene.

Family *incertae sedis*: *Morotopithecus bishopi*, a very recently discovered hominoid species from the Moroto site in Uganda, dates to 20.6 Ma (Gebo *et al.* 1997). Little is known of the palaeoenvironments associated with this species. Dental evidence, recovered separately from the most recent postcranial finds, helps to substantiate two claims regarding this fossil primate: 1) dentally, it demonstrates a primitive catarrhine dental pattern (a pattern which was likely associated with a frugivorous way of life), and 2) it was a very large hominoid with an estimated body weight ranging from 30 to 62 kg (Gebo *et al.* 1997). Elements of the postcranium reveal a distinctly hominoid-like morphology for *Morotopithecus*. As Gebo *et al.* (1997, p. 402) explain, this hominoid represents "...an arboreal primate that moved using climbing, a slow to moderate speed of

brachation, and quadrupedalism, and utilized an arm-hanging posture". As Bower (1997) cites, in spite of its early appearance in the fossil records, this species may be said to be the earliest and clearest representative of a form ancestral to extant hominoids (also Gebo *et al.* 1997).

Early-Middle Miocene - African Hominoids:

Oreopithecidae* (18-14Ma):* This family constitutes two distinct genera *Nyanzapithecus* and *Mabokopithecus* (McCrossin 1992; McCrossin and Benefit 1994). All species (3 total) attributed to these genera have been found in Kenya at the sites of Rusinga Island (i.e., *Nyanzapithecus vancouveringi*) and Maboko Island (i.e., *Mabokopithecus clarki* and *Nyanzapithecus pickfordi*)(McCrossin 1992; Andrews *et al.* 1997). While Rusinga Island likely experienced forested conditions during much of the early-mid Miocene, palaeoenvironmental evidence supports that this site experienced greater seasonality and aridity when compared with earlier, more forested primate sites (i.e., Songhor and Koru) (Andrews *et al.* 1997). While some contend that the environmental conditions at Maboko Island were densely wooded (i.e., Harrison 1992), more recent views maintain that the palaeoenvironments were likely dominated by dry woodland areas (Andrews *et al.* 1997). Dental remains are scarce for these hominoids, however, there is sufficient evidence to support that these oreopithecids were predominantly folivores (McCrossin 1992; Fleagle 1988). Postcranial elements of the forelimb indicate that these hominoids displayed adaptations consistent with scansorial and climbing abilities suited to an arboreal way of life (McCrossin 1992). In fact, before the discovery of *Morotopithecus* it was suggested that the postcrania of oreopithecids provided the first real glimpse of a distinct arm-swinging mode of locomotion much like that observed among extant hominoids.

***Afropithecus* (~17Ma):** The family designation of this genus is uncertain, but increasingly evidence favours a close affinity between *Afropithecus* and *Proconsul* (Leakey and Walker 1997). The sites associated with *Afropithecus* are located near west Lake Turkana, Kenya. To date, very little has been done in regards to the reconstruction of the palaeoenvironments of these sites (Andrews *et al.* 1997). Afropithecines were fairly large animals with an average body weight estimated at 34-36 kg (Leakey and Walker 1997). Postcranially, these hominoids are strikingly similar to *Proconsul* insofar as their limb morphologies indicate a "...relatively deliberate, even-limbed quadrupedal arboreal animal that lacked overt specializations for arm-swinging or terrestrial locomotion, or leaping" (Leakey and Walker 1997, p. 233; Rose 1994). The cusp morphology and lack of molar cresting in *Afropithecus* strongly hints that these fossil apes were frugivores (Andrews and Martin 1991; Leakey and Walker 1997). However, more derived features relating to dentition, i.e., a thickening of the molar enamel, hints that there may have been a subtle, although as yet poorly understood, change in the afropithecines' dietary regime (Andrews and Martin 1991).

***Kenyapithecus* (~14-16Ma):** Two distinct species are currently recognized within this genus, *K. wickeri* and *K. africanus* (McCrossin and Benefit 1993,1997). The regional distribution of these two species is restricted to the Kenyan sites of Fort Ternan and Maboko Island. As mentioned above, the palaeoenvironments associated with the Maboko sites are generally thought to consist of dry to semi-dry forests. By contrast, Fort Ternan palaeoenvironments appear to represent a more mosaic environment, consisting largely of closed canopied woodlands with intermittent areas of more open woodland, grassy glades along with a few areas of dense vegetation (Shipman 1986; Pickford 1987b; Kappelman 1991; Harrison 1992; Andrew *et al.* 1997).

Dental evidence for these species has been used to support that these hominoids subsisted on a diet composed largely of hard food items such as nuts, seeds and hard fruits

(McCrossin and Benefit 1993, 1997; Benefit and McCrossin 1995). As McCrossin and Benefit (1993,1997) explain, derived dento-gnathic features possessed by these kenyapithecines, including enlarged incisors (as required for incisal preparation of hard shelled/skinned fruits) and thickened enamel (as required to grind course, hard foods), are thought to be good indicators of such a hard-object dietary regime. In light of the apparent increase in seasonality and the decrease in the distributions of densely forested areas, such dietary changes have typically been attributed to a more terrestrial way of life. Previously post-cranial remains were thought to evidence greater degrees of terrestrial quadrupedalism among these hominoids (Benefit and McCrossin 1995; McCrossin and Benefit 1997). Indeed, primitive catarrhine retentions in both the fore- and hind limbs suggest a pattern of locomotion (including slow quadrupedalism - both terrestrial and arboreal - and climbing) very similar to cercopithecoid and other monkeys (McCrossin and Benefit 1994). While such characteristics possibly foreshadow adaptive specializations unique to only great apes and humans, such dental and postcranial features more firmly support the placement of kenyapithecines into a phylogenetic position ancestral to *all* hominoids (hylobatids and great apes) as well as humans. In other words, "...*Kenyapithecus* and other large-bodied hominoids of the middle to late Miocene ...were merely avatars, not ancestors, of the extant great apes" (McCrossin and Benefit 1994, p.111).

However, as Gibbons and Culotta relate (1997), very recent discoveries can be used to support that *Kenyapithecus* may, in fact, be the closest African ancestor to great apes and humans *alone* (see also McCrossin 1997). A recently recovered humerus reveals a shaft much straighter than other previously found humeri (McCrossin 1997). Such a humeral configuration supports that the locomotor adaptations of these mid-Miocene hominoids were more fore-limb dominated and, consequently, that the locomotor repertoire of kenyapithecines was likely less reliant on semi-terrestrial quadrupedalism

than previously thought (McCrossin 1997). In conjunction with the humerus, elements of the forelimb were also said to reveal a more distinctly hominoid-hominid configuration. The distal aspects of the tibia, as well as elements of the calcaneous and the cuboid, support that these kenyapithecines were able to significantly rotate (eversion and inversion) their feet. With such morphological adaptations it is postulated that kenyapithecines would have been conferred a tremendous advantage in, not only arboreal climbing, but also in terrestrial walking (McCrossin 1997; Gibbons and Culotta 1997).

***Otavipithecus* (13Ma):** Great debate exists regarding the phylogenetic placement of this genus (see Conroy 1994 *contra* Begun 1994a). In many respects, of which geological and temporal placement are not the least, this fossil ape is very enigmatic (Conroy *et al.* 1993). Today the ecological setting of the *Otavipithecus* site (Namibia) is very dry, bordering on extreme desertic conditions. However, it is postulated that during the mid to late Miocene the conditions were milder and more humid, possibly culminating in a forested biome (Conroy *et al.* 1993). As Conroy *et al.* (1993) relate, dental evidence supports that this hominoid retained the primitive catarrhine dentition consisting of low-crowed, non-crested, thin-enamelled molars. Such a dentition would invariably have occurred in conjunction with a diet of soft, non-abrasive food items such as ripe fruit. Portions of a proximal humerus have been attributed to *Otavipithecus*. Although very fragmentary, these remains do suggest that the locomotor capacities of these hominoids were quite primitive relative to the more derived conditions expressed in extant hominoids (Conroy *et al.* 1993).

Early to Mid Miocene - African Cercopithecoids:

***Victoriapithecidae* (19-14 Ma):** This family consists of two distinct genera, *Victoriapithecus* and *Prohylobates* (McCrossin and Benefit 1994). The phylogenetic position of this family remains uncertain. However, the retention of certain primitive

catarrhine characteristics combined with the expression of derived cercopithecoid-like features has lent increasing support to the understanding that this primate family is an ancestral sister group to the later appearing family Cercopithecidae (i.e., colobines and cercopithecines) (Delson 1975; Harrison 1987; Benefit 1993; Benefit and McCrossin 1993). Sites associated with Victoriapithecidae are found throughout east Africa, predominantly in Uganda (Napak site, the earliest know true cercopithecoid at 19 Ma) , Egypt and Kenya (Harrison 1992; McCrossin and Benefit 1994). While it is claimed that few of these sites coincide with fossil hominoid discoveries, it is important to note that a great majority of all victoriapithecids have been found at the Maboko site, and are relatively contemporaneous with *Kenyapithecus* (Benefit and McCrossin 1989; Harrison 1992; Benefit 1993; McCrossin and Benefit 1994). Evidence suggests that the appearance and proliferation of Victoriapithecidae in western Kenya occurred in conjunction with the Maboko heating event at 17.5 Ma (Pickford 1987c). The ultimate consequence of such an event would have been an expansion of dryer, more open woodland areas (Senut 1987; Andrews *et al.* 1997). Dental evidence for victoriapithecids demonstrates a mosaic of features. Compared to the dental morphotype exhibited by extant cercopithecoids (i.e., high-crowed, sharply crested, bilophodont molars), the teeth of Victoriapithecidae are fairly low crowned. Incipient bilophodonty is apparent, however (Benefit 1993; McCrossin and Benefit 1994). The shape of the molars, in conjunction with the shape of incisors, suggests that these early Old World monkeys were likely adapted to a diet based less on ripe fruits, and more on tough-skinned fruits and seeds (McCrossin and Benefit 1994). As McCrossin and Benefit (1994) explain, postcranial evidence largely supports that victoriapithcids were semi-terrestrial in their locomotor adaptations. However, these adaptations towards terrestriality might not have been of a uniform kind, but rather of many degrees, with

some species spending more time on the ground that other more arboreally-based species (Fleagle and Kay 1985; Senut 1987).

***Microcolobus* (?14-8.5 Ma):** *Microcolobus* is the one of the few cercopithecoid monkeys known to have existed in the mid Miocene of east Africa prior to the emergence of extant Old World monkeys (Pickford 1987a, 1987c). This genus is thought to represent an intermediate link between Victoriapithecidae and Colobinae, and is likely ancestral to extant colobines. These monkeys are found at the Kenyan sites of Ngeringerowa, Ngorora and Nakali (Benefit and Pickford 1986). Appearing after the end of the mid-Miocene cooling event (see Pickford 1987c), it is likely that the palaeoenvironments of these monkeys were quite open and arid. Only cranio-dental evidence is available for this species. Based on dentition, it has been suggested that this was a very small-bodied monkey exhibiting features less derived (i.e., low-cusped teeth) compared to extant colobines . As the teeth document, this small monkey was likely an eclectic feeder, invariably feeding off less leafy-matter than extant colobines (Benefit and Pickford 1986).

Early to Mid Miocene - Eurasian Hominoids:

European *Pliopithecidae* (~17-15? Ma): *Pliopithecus* is believed to be one of the first hominoid species to have migrated out of Africa towards the end of the early Miocene (Harrison 1987; Harrison *et al.* 1991). As Harrison (1987; also Harrison *et al.* 1991) relates, there may have existed as many as four different genera (*Pliopithecus*, *Crouzelia*, *Anapithecus* and *Plesiopliopithecus*) within this family. Further, these authors maintain that the dispersal of this family throughout Europe (and later Asia) was extensive, occupying areas of western (i.e., France), central (i.e., Germany, Switzerland) and eastern (i.e., Czechoslovakia) Europe. Until as recently as 10 Ma, these regions were predominantly subtropical seasonal forest and woodland biomes (see Andrews *et al.*

1997). Dental evidence suggests that these pliopithecids were likely eclectic feeders. Some molar samples reveal only very moderate shearing crests which hints that some pliopithecids maintained a predominantly frugivorous diet. By contrast, other molars express significantly greater cresting, which suggests that there was a tendency among some genera towards increased folivory (Kay and Ungar 1997). Fossil postcrania for Pliopithecidae, especially that of the forelimb, appears to be very similar to *Dendropithecus*. From such evidence it can be concluded that these catarrhines were exclusively arboreal, employing a large degree of quadrupedal suspensory activity in relation to locomotor and positional behaviours (Rose 1997).

Saudi Arabian *Heliopithecus* (~17 Ma): During this period of the early Miocene, a large portion of North Africa remained docked to the Arabian peninsula (see Tchernov 1992). The appearance of *Heliopithecus* in Arabia at this time is likely attributed to this connection. Palaeoenvironmental conditions in Arabia at this time, while they likely remained relatively humid and lush (i.e., rain forests and dense woodland areas), were said to have been progressing towards drier, more open conditions (Tchernov 1992). Although the fossil evidence for *Heliopithecus* is meager, what little is available does suggest some possible affinities with the African hominoid *Afropithecus* (Andrews 1992a; Leakey *et al.* 1995a; Leakey and Walker 1997). Cusp and crown morphology suggest that these hominoids were predominantly frugivorous, while a thickening of the molar enamel can be used to support a change in the dietary regime towards a greater component of hard-object feeding (Leakey and Walker 1997).

Mid to Late Miocene - Eurasian Hominoids:

Turkey, *Griphopithecus* (~15 Ma): The only fossil remains associated with *Griphopithecus* have been found in Pasalar, Turkey. During the mid Miocene it is estimated that the palaeoclimate was likely subtropical (with a pronounced dry season) at

this Pasalar locality (Bernor and Tobien 1990; Andrews 1990; Andrews *et al.* 1997). While fossil remains for this species are scant, postcranial evidence supports that this hominoid was a very large, arboreal quadruped (Andrews *et al.* 1997). In many respects this species is thought to display many characteristics highly reminiscent of kenyapithecines (Andrews 1992a).

***Sivapithecus* (~13-6.8 Ma):** Great controversy surrounds this genus. A major source of contention is the regional distributions of these very large bodied hominoids. There is evidence to support that the geographic range of sivapithecines was large, extending from Europe (i.e., Greece and Turkey) to India and Pakistan, throughout South Asia, and finally to China (Andrews 1983; Ward 1997). However, the greatest amount of evidence has come from the Siwaliks formation in Pakistan (Ward 1997). As with geographic range, there was a tremendous range in the palaeoenvironments occupied by these hominoids. Most of the earlier sites were likely in wooded habitats in a tropical or subtropical climate (Andrews 1990; Andrews *et al.* 1997). However, in later sites a dryer, more seasonal climate along with a more open forest-woodland environment likely came to prevail (Andrews *et al.* 1997; Ward 1997). Molar evidence (i.e., large, low reliefed molar crowns covered with thick enamel) suggests that these hominoids subsisted on a diet of hard-shelled fruits and nuts. Post cranial elements demonstrate that this very large primate (~46-64 kg) invariably practiced some form of quadrupedalism (possibly terrestrial, but more than likely arboreal) with very little suspensory locomotion (Andrews 1983; Rose 1989; Andrews *et al.* 1997; Rose 1997).

Germany, *Paidopithex* (~ 11.5 Ma or MN 9, see Appendix B for epoch conversion): As was the case for much of Europe at this time, the palaeoenvironment in Germany was invariably subtropical and seasonal. A complete femur, found at the Eppelsheim site, is attributed to *Paidopithex* (Begun 1992a). As Begun (1992a) relates, the long, gracile build of this femur is highly reminiscent of *Pliopithecus*, and suggests

that the locomotor behaviours of these hominoids were markedly quick and agile, much like New World cebids, especially *Allouatta*. Further, Begun suggests that these hominoids likely engaged in a more "primitive" mode of locomotion dominated by suspensory quadrupedalism with a limited amount of below-branch suspension.

Austria, *Austriacopithecus* (~ 13-14 Ma or MN 8): Humeral shafts and an ulna, found in the Klein Hadersdorf region of Austria, represent this genus (Begun1992b). These post-cranial elements suggest that this hominoid retained a morphology similar to *Kenyapithecus* and, consequently, was restricted in its locomotor capacities to an above-substrate quadrupedalism, either terrestrial and/or arboreal (Begun 1992b; Rose 1997).

***Dryopithecus* (~15-11 Ma or MN9-8/7):** The bulk of all fossil evidence relating to *Dryopithecus* has been found in Spain (Can Llobateres and Can Ponsic sites), Hungary (at Rudabanya) and France (St. Gaudens). The palaeoclimates associated with each of these sites are believed to have been predominantly subtropical in nature, and the local environments were likely seasonal, humid subtropical forests (Begun *et al.* 1990; Andrews *et al.* 1997). The thin enamelled and high crowned teeth associated with dryopithecines have been cause for some debate as to the diet of these hominoids. Some have suggested that these dental attributes provide evidence that some component of folivory was included in the diet of dryopithecines (see Begun 1994a). More recently, others have concluded that the shearing-crests observed on *Dryopithecus* molars preclude any form of hard-object feeding or extreme folivory, and instead support that these hominoids consumed mostly soft fruit (Kay and Ungar 1997). Generally thin dental enamel is thought to represent a condition primitive to the derived hominid morphotype. However, those who support a close relationship between European drypothecines and "true" hominoids suggest that thin enamel among these hominoids might be best explained as a homoplastic feature which evolved independently of other, more distinctly

hominid features (Begun 1997). Indeed, the ancestral relationship of dryopithecines may only be fully realized once factors of homoplasy/convergence are recognized as the norm rather than the exception in Hominoid evolution.

Post-cranial elements can be used to further substantiate the close ancestry of *Dryopithecus* to hominoids, especially African apes and humans. Unlike cranio-dental evidence which suggests parallel development, these post-cranial elements tends to support ancestral relationships based on s*hared derived features* similar to extant hominoids. Forelimb elements, including humeral shafts, a radius and ulna, lunate, hammate and phalanges, together with hindlimb components (i.e., metatarsals and phalanges) are said to express a number of unique features which distinguish these apes from the more primitive catarrhine morphotype (i.e., quadrupedalism), while at the same time they closely align *Dryopithecus* with extant hominoids (Begun 1992b; Rose 1997; Ward 1997). While the post-cranium does reveal that a certain degree of quadrupedal locomotion likely continued to be employed by these apes, it provides greater evidence that *Dryopithecus* was involved in more extensive suspensory behaviours (Begun 1992b; Rose 1997). While much of this suspensory activity may have been quadrupedal, there is increasing evidence which suggests that suspension was forelimb dominated. A very recent find of *Dryopithecus* (i.e., *Dryopithecus laietanus*) from Can Llobateres, Spain provides very stong evidence in favour of extensive suspensory behaviours. As Moya-Sola and Kohler (1996) relate, this partial skeleton provides many indications of suspensory behaviours in its trunk morphology (i.e., configuration of the thoracic and lumbar vertebrae, and the overall broad shape of the thorax), and fore- and hind limb morphologies (i.e., an intermebral index approaching, or perhaps even exceeding that of extant African apes, as well as a great number of features associated with the hominoid morphotype and the proclivity towards forelimb domination in locomotor and feeding behaviours- consult Appendix A). Consequently, such a change in the behavioural

repertoire of these European hominoids may be attributable to a distinctly hominoid-hominid morphological/adaptive configuration and, as such, may prove to be of great utility in substantiating the ancestral position of dryopithecines to later large body hominoids (i.e., African Apes and humans to the exclusion of Asian forms) (Begun 1992b; Begun *et al.* 1997).

***Ouranopithecus* (~11-8.5 Ma or late Vallesian to earliest Turolian):** Specimens attributed to this genus are isolated to regions of northern Greece. While during the latter portions of the Miocene the palaeoenvironment of all Greece was likely a mosaic of conditions ranging from open savanna to more forested regions, sites associated with *Ouranopithecus* are said to be more consistent with dry and open savanna conditions (DeBonis *et al.* 1992; DeBonis and Koufos 1994, 1997; Andrews *et al.* 1997). The overall body size of this hominoid is predicted to have been very large, and appears to exhibit a range in size and dimorphism very similar that of *Gorilla gorilla* (DeBonis *et al.* 1990; DeBonis and Koufos 1994, 1997; Koufos 1995). A great number of *Ouranopithecus* specimens have been recovered and are represented only by cranio-dental remains. Certain features hint at the "primitive" African ancestry of these apes (Andrews 1990a). As DeBonis and Koufos (1993) explain, aspects of the upper premolars and a definite thickness of the molar enamel may be said to be a derived feature shared with/inherited from *Kenyapithecus*. The retention of thick molar enamel among *Ouranopithecus* would have conferred great advantage to these apes. Increasing aridity and greater open, non-forested areas likely would have affected a transition from a dietary regime based on the consumption of soft fruits, leaves and buds to one based almost exclusively hard, course objects such as nuts and seeds (DeBonis and Koufos 1997). However, while features of the molar configuration may hint at primitive ancestry, they may also be used to provide strong support for a more derived condition. Consequently, certain aspects of the molar morphology are often thought to reveal a very

close affinity between *Ouranopithecus* and Plio-Pleistocene hominids (DeBonis and Koufos 1997) . Using such dental data, there is definite support for the notion that the split between African apes and the human line could have occurred much earlier than dates upheld by molecular clocks (5 Ma, see Cronin 1983), and perhaps could have occurred as early as 12 Ma (DeBonis and Koufos 1993). DeBonis and Koufos (1993) support that in Europe, specifically Greece, a sister group to all true hominids, as represented by *Ouranopithecus*, may have been present by 10 Ma . Shared derived features of cranio-dental elements, including a reduction in canine size, a rounded base on the canines, a lack of a P3 honing surface, short and broad homomorphic premolar crowns, thick enamel, and a more vertically oriented facial profile, to name only a few features, all help to build a persuasive argument in favour of a close relationship between *Ouranopithecus* and later hominids (DeBonis and Koufos 1993, 1994, 1997).

***Oreopithecus bambolii* (~10-6 Ma or MN 12-14):** Found in Baccinello, Italy, this species is generally associated with palaeoenvironments suggestive of humid, swamp-like forested conditions (Andrews *et al.* 1997; Harrison and Rook 1997). While in the past it has generally been thought that this hominoid descended from early Miocene oreopithids in Africa, an increasing body of evidence supports that, in fact, *Oreopithecus bambolli* evolved within Europe from a generalized ape morphotype (McCrossin 1992; Harrison and Rook 1997). Dental evidence reveals that the molar cresting and shearing capacities among *Oreopithecus bambolii* appear to have reached their highest expression compared to all other European hominoids, suggesting that these were the most folivorous of all European apes (Kay and Unger 1997). Post-cranial evidence presents a confusing mix of very derived and very primitive features. The forelimb indicates that this hominoid was an adept suspensory arborealist, showing highly derived features as found only in extant hominoids (Rose 1997; Ward 1997; Harrison and Rook 1997). The hindlimb, by contrast, demonstrates a morphology more typical of earlier, more primitive

hominoids (Ward 1997). In light of the above information, it can be seen that this species is very enigmatic in relation to its taxonomic and phylogenetic position. Much of the confusion surrounding this species may be attributable to the high degree of intra-specific variation it expresses (Rook *et al.* 1996).

Late Miocene - Pliocene Cercopithecoids:

Africa: Towards the close of the Miocene, the climatic conditions throughout Africa were marked by increasing aridity and more open desert-like environments. Such conditions reached their climax with the Messinian Crisis at approximately 5 Ma (Tchernov 1992). Towards the end of the Miocene, it may have been that many mammalian groups in northern and eastern African were becoming increasingly more adapted to such severe environmental conditions (Tchernov 1992). Pickford (1987c) postulates that a resurgence of cercopithecoids, or more specifically cercopithecoids of modern aspect, took place at some time around 12 Ma . The earliest cercopithecoids to reappear are generally attributed to distinctly colobine species. Monkeys attributed to the Papionini tribe are predicted to have emerged at some time around 8 to 10 Ma, while member of the Cercopithecini tribe likely emerged some time later around the Miocene-Pliocene boundary (Pickford 1987a, c). Such papioninis and cercopithecinis (e.g., *cf. Libyapithecus sp.*, *"cf. Mesopithecus"*, and *cf. Macaca sp.*) are attributed to sites in Northern Africa, and are generally found in association with colobine monkeys (i.e., ? *Colobus*, *Paracolobus chemeroni*) (Geraads 1987; Pickford 1987c). All of these fossil cercopithecoids from these north African sites, including regions of Egypt, appear to be closely related to species found in regions of sub-saharan Africa (Geraads 1987). Invariably, these extinct cercopithecoids more closely resembled, both behaviourally and morphologically, modern cercopithecoids than did earlier Miocene monkeys (i.e., *Victoriapithecus* and *Prohylobates*) in east Africa (Strasser and Delson 1987). The

continued effects of sub-saharan desiccation and desertification within Africa at the end of the Miocene are believed have prompted a radiation and outward migration of many mammalian species, of which cercopithecoids were definitely a significant part (Pickford 1987a,c; Tchernov 1992). In spite of large-scale migrations, many cercopithecoid species persisted in Africa, and likely achieved those morphological configurations attributed to extant Old World monkeys sometime during the Pliocene epoch (Harrison and Harris 1996). Many cercopithecoids migrated out of Africa and into Asia via the Arabian peninsula (see Barry 1987; Whybrow *et al.* 1990). However, the earliest migrations yet documented are those which took these monkeys into Europe.

Europe: Climatic conditions in Europe remained mild and subtropical throughout the late Miocene and into the Pliocene. The latitudes of subtropical seasonality likely extended 10-15 degrees further north than their current placement (Pickford 1987a). The first cercopithecoids to appear in Europe belongs to the genus *Mesopithecus* (Ardito and Mottura 1987). These monkeys were wide spread in south and central Europe between 11-6 Ma and appear to have been in fairly close association, both spatial and temporal, with certain late Miocene Hominoids (i.e., *Ouranopithecus*) (Delson 1975; Ardito and Mottura 1987; Koufos *et al.* 1991). While overall these fossil monkeys appear most similar to extant colobines (see subfamily classification proposed by Strasser and Delson 1987), they exhibit an interesting morphological mosaic which may indicate otherwise. The cranio-dental evidence associated with *Mesopithecus* is very similar to the extant colobine condition and, therefore, may indicate a predominantly folivorous diet (Szalay and Delson 1979; Ardito and Motturo 1987). Postcranially, however, this cercopithecoid expresses a strong component of terrestrial or semi-terrestrial adaptation . Such adaptations appear to be convergent with a more cercopithecine-like mode of locomotion (Szalay and Delson 1979; Ardito and Motturo 1987). However, there are some indications that earlier representatives may have been

more arboreal (Szalay and Delson 1979). Later forms likely evolved in response to changing environmental conditions and increases in competition. Consequently, morphological adaptations would have evolved to facilitate terrestrial feeding and inter-patch dispersal (Szalay and Delson 1979). *Dolichopithecus*, a second group of early European colobines, is associated with the late Miocene to mid Pliocene in southern Europe (Ardito and Motturo 1987). These monkeys are considerably larger than earlier *Mesopithecus* and express a greater tendency towards terrestrial locomotion. Dentally it appears that these cercopithecoids were very colobine-like (Delson 1975; Szalay and Delson 1979).

The later Mio-Pliocene and Pleistocene saw a great influx of monkeys, predominantly cercopithecines into Europe. *Paradolichopithecus* appears in south western Europe during the Villefranchian period, or 2 to 3 Ma (Delson 1975; Ardito and Motturo 1987). In most respects, cranio-dentally and post-cranially, this monkey appears to be the first European representative of a cercopithecine stock (Delson 1975; Ardito and Motturo 1987). Finally, *Macaca* appears much later in the Pleistocene. Cercopithecines appears to out-live all other cercopithecoids during this epoch, likely because of their abilities to adapt to the severe climatic and environmental conditions imposed during the Pleistocene (Delson 1975; Ardito and Motturo 1987).

Latest Miocene to Earliest Pliocene - Possible Hominids from East Africa:

In Africa, between 14 and 4 Ma, there exists only a relatively small number of very fragmentary remains that may, or may *not*, be attributable to a hominoid/hominid clade (consult Hill and Ward 1988; Hill 1994, 1995 for a detailed look at these finds). For the purposes of this paper most of this evidence is considered to be far too ambiguous. Consequently, only a select few of the youngest, most "hominid-like" fossils will be discussed.

Lukeino Formation (~6.2-5.6 Ma): This specimen, found in the Tugen Hills region of Kenya, consists of a what is thought to be a single, unerupted, left mandibular molar possibly belonging to one of the earliest species of hominid yet discovered. The crown and cusp configurations of this tooth are very low and of minimal relief (i.e., "obtuse"). The "Y" fissure pattern suggests that this tooth is of a distinct and definite hominoid type, especially *Pan*-like, and may represent the ancestral morphotype of humans and chimpanzees (Hill and Ward 1988; Hill 1994; Wolpoff 1997).

Lothagam Formation (~5.5 Ma): The palaeoenviroments of this region are thought to have been dominated by comparably open, riparian woodland and grassland areas (Leakey *et al.* 1996). The specimen found at this Kenyan site is a mandibular fragment consisting of a single molar (M1) and a segment of the alveolar region (approximately from P4 to M3) (Hill and Ward 1988; Hill 1994). Much study on this specimen has led to the general consensus that it shares distinct, derived features (i.e., squared molar shape, serrate root formation indicating great masticatory power, a thicker and taller mandibular body and evidence of decreased prognathism in the lower jaw, to name just a few of the many metric feature) which link it strongly to *Australopithecus afarensis* (Kramer 1986; Hill and Ward 1988; Hill 1994; Wolpoff 1997). However, other, more recent anaylses tend to support that certain features of this hominoid express only minimal similarities with species of *Australopithecus afarensis* (White 1986). In fact, the Lothgam mandible may show greater affinities with more recent finds (i.e., *Australopithecus ramidus,* as will be discussed later)(White *et al.* 1994).

Tabarin Specimens from the Chemeron Formation (~5.1-5.0 Ma): Evidence from this Tugen Hills site consists of a mandible and portion of a proximal humerus. In many respects the mandible is metrically and visually very similar to that of Lothagam. Such characteristics may be used to place this specimen in a position very near to the *A. afarensis* morphotype. Tooth morphology is very derived in respect to the thickness of

the molar enamel and the low relief of the molar crown. Root morphology, as with Lothagam mandibular roots, suggests a high degree of masticatory stress/power. The proximal humerus appears to show many distinctly hominid characteristics including an elliptical, antero-medially oriented humeral head and deep intertubercular groove - all of which tend to indicate a decreased reliance on arboreal, ape-like climbing locomotion (Hill and Ward 1988; Hill 1994).

Aramis, Ethiopia (~4.4 Ma): Seventeen fossil specimens, representing cranial and post-cranial regions, have been discovered at this site (White *et al.* 1994). This evidence presents an interesting and unique suite of features among the earliest possible "hominids". Consequently, these recently discovered, unique fossils have been assigned to a new species, *Australopithecus ramidus*. Others even suggest that these finds may be better placed under a new generic designation, *Ardipithecus* (White *et al.* 1995). It has been determined that these early hominoids very likely lived in a forested environment (WoldGabriel *et al.* 1994). In terms of overall morphology, all evidence indicates that these Mio-Pliocene hominoids were small compared to later australopithecines (White *et al.* 1994). In many respects, these hominoids appear to have been more similar to chimpanzees than humans in their cranio-dental and postcranial morphologies. Dentally, evidence from the canines (i.e., larger canines) and molars (i.e., thin enamel) hints at a close affiliation between these early hominoids and chimpanzees. Postcranial evidence of *A. ramidis* suggests a mosaic of features which are both ape-like and hominid-like (White *et al.* 1994) . While no definitive conclusions have been reached in regards to these hominoids' locomotor pattern, it can be fairly assumed that they exhibited locomotor behaviours somewhere between ape arborealism and hominid terrestriality.

Kanapoi and Allia Bay (~4.2 - 3.9 Ma): Numerous elements have been discovered at these sites and are likely representative of a unique hominid species *Australopithecus anamensis* (Leakey *et al.* 1995b). The palaeoenvironments associated

with these hominids are believed to have been relatively open, dry wood/bush lands (Leakey *et al.* 1995b). The size of this hominid has been estimated at 55 kg (Wolpoff 1997). In many respects, cranio-dental evidence supports that *A. anamensis* was similar to later, more derived *A. afarensis* (i.e., thicker molar enamel). However, larger canines and premolar morphology suggest a more primitive affiliation (Leakey *et al.* 1995b). Aspects of the tibia provide strong support for the idea that these hominids were well on their way towards incorporating bipedality, possibly obligate, into their locomotor repertoire (Leakey *et al.* 1995b; Wolpoff 1997).

East and South African Sites (3.7 Ma ....): The first "true" hominid morphotype may be best attributed to *Australopithecus afarensis*. This species, although it is generally thought to have been east African in its occupation (e.g., Laetoli and Hadar), may also have ranged into South Africa (Clark and Tobias 1995; Wolpoff 1997). It is generally agreed upon that the regional environments of *A. afarensis* were becoming increasingly more arid and open. Cranio-dental evidence shows a distinctly hominid configuration (i.e., a reduction in canine size, a tremendous thickening of enamel, larger premolar and molar sizes, to name a few) (Wolpoff 1997). Post-cranially, these hominids were indisputable bipeds (i.e., pronounced heel strike, medial foot arch, adducted first metatarsal, etc.) (Clark and Tobias 1995; Wolpoff 1997). However, it is debated whether this bipedality was one of an absolute kind, or rather one of degree wherein these hominids maintained a certain reliance on an arboreal way of life (Jungers 1994).

As the above review of the fossil evidence reveals, Miocene hominoids, both within and outside the confines of Africa appear to demonstrate a tremendous mosaic of features. The next chapter will attempt to make sense of this mosaic by revealing what environmental/ecological trends can be shown to have paralleled or prompted the adaptation and evolution of these Miocene hominoids.

Chapter Four
The Plot Unfolds: A Synthesis

The preceding chapters have provided a comprehensive review of the fundamental principles of ecology and Ecosystematics (Chapter One), their basic relevance to (palaeo) primate studies (Chapter Two), and their specific or inferred manifestations (i.e., palaoevironmental/ecological reconstructions and their behavioural/morphological implications) in the fossil records (Chapter Three). The aim of this chapter is to synthesize all of this information towards the end of developing a more clear and concise picture of the patterns and processes of hominoid evolution from an Ecosystematic perspective. This chapter will look at the degree to which climatic and ecological variability from the latest Oligocene through to the early Pliocene effected 1) resource availability, 2) inter- and intra- populational stress (i.e., competition), 3) niche differentiation and/or niche exclusion, 4) migratory trends, and 5) ultimately, patterns of hominoid/hominid evolution.

Latest Oligocene and Early Miocene

As discussed in previous chapters, it is in east Africa, during the latest Oligocene and earliest Miocene, that the first evidence for true hominoid adaptation and evolution has been traced. From 27 Ma to 17 Ma, climatic and ecological conditions are believed to have been very consistent (Barry *et al.* 1985). During this period east Africa was dominated by densely forested, resource-rich environments. In these tropical biomes, overall climatic stability would have ensured a constant and even input of water and solar energy into the ecosystem. As such, a large and diverse base of primary energy producers (i.e., plant resources) would have prevailed and, consequently, would have been readily available for exploitation by a number of secondary energy producers (i.e., animal and

other consumers). A diversity of primary energy sources would have supported equally diverse/speciose *communities* of consumers. As explained in Chapter One, while tropical biomes may promote species diversity, the absolute number of individuals belonging to each species, and occupying each niche will remain relatively low. Small populations will be maintained so as not to over-exceed the carrying capacity of their niches or to over-exploit the preferred resources therein. In such tropical conditions, there will tend to be a high degree of niche differentiation and specialization. In keeping with Gause's rule (i.e., that no two species can coexist in the exact same niche), species will differentiate in their patterns and methods of resource exploitation so as to avoid, not only conspecific competition, but also excessive levels of interspecific competition.

During the latest Oligocene, the first hominoid primate, *Kamoyapithecus*, is said to have first appeared (Leakey, Ungar *et al.* 1995). To date, very little is known about this genus, its species diversity, its distribution or specific palaeoenvironment. However, it can be safely inferred that this hominoid lived in a very lush, tropical environment. Further, as there is an obvious lack of other primates found in association with *Kamoyapithecus*, it may also be safely assumed that this hominoid was likely not subjected to the stresses of competition. After *Kamoyapithecus*, the next, major epoch of hominoid emergence and evolution was the Miocene.

In specific regard to early Miocene hominoid adaptation and evolution, we see direct manifestations of the general rules of ecology outlined above. The earliest hominoids in east Africa are those belonging to the family Proconsulidae. Species diversity among this family was extremely great, with six genera and many more species represented. While there is no sure way of predicting how large the population groups for each species were, following the general ecological trends, we may assume that they were very likely small. *Morotopithecus* is relatively contemporaneous with these early Miocene proconsulids. As there is little known about this hominoid genus (i.e., the

number and kinds of species that may have been associated with it), it is impossible to say anything about its levels of species diversity. However, what is of tremendous import in regards to the discovery of this species is that it represents a fairly distinct morphotype from all other early Miocene hominoids.

The high levels of diversity (at the family, generic and species levels) among these early hominoids would have posed tremendous stress for these apes had niche overlap been unavoidable. However, referring back to Chapter Three, palaeoenvironmental and morphological evidence supports that each species would have been able to avoid excessive competition by virtue of niche, behavioural and morphological differentiation. In terms of environmental use, while all these early hominoid species occupied predominantly tropical/forested habitats, evidence suggests that there was a differential use of the space and resources in these tropical biomes. For example, *Dendropithecus* likely monopolized semi-dry upland forests while, in contrast, *Proconsul* species probably ranged over more diverse/mosaic environments (Retallack *et al.* 1995).

In terms of behaviour, the dental evidence of *Rangwapithecus* and *Simiolus* supports that only these two genera evidence any sort of tendency towards folivorous behaviours. In contrast to *Rangwapithecus* and *Simiolus*, the majority of early Miocene hominoids (i.e., *Dendropithecus*, *Proconsul*, *Micropithecus*, *Limnopithecus*, and possibly *Morotopithecus*) appears to have relied on diets based on fruit resources, or more specifically *ripe* fruit resources. Even within the a rich, tropical biome, such fruit resources may have been of restricted availability to these apes. Such restrictions would have been compounded by any levels of competition among these apes for the same ripe fruit resources. However, post cranial evidence for these early Miocene frugivores suggest that any potential for excessive competition for ripe fruits was avoided through differential means of procurement. While some hominoids may have maintained a primitive form of arboreal quadrupedalism as a means of accessing fruit resources (i.e.,

Proconsul), others (i.e., *Morotopithecus* and *Dendropithecus*) would have accessed those ripe fruits unavailable to arboreal quadrupeds. For these latter arboreal primates, bouts of terminal branch feeding, as made possible through locomotor and positional behaviours including arm-hanging and quadrupedal suspension, would have facilitated their access to hard-to-reach food items.

Early Middle Miocene

From 17 Ma to 15 Ma a major change, or at least a series of minor climatic and environmental perturbations are believed to have occurred in east Africa (Barry *et al.* 1987; Tchernov 1992). The overall trend was towards increased aridity and some degree of environmental desiccation (Tchernov 1992). However, as discussed in Chapter Two, the shift towards increased aridity was not abrupt. Decreased levels of water in the tropical ecosystems would have reduced the total amount of resources available to the various consumer groups in east Africa. As tropical regions gradually began to transform into a mosaic of more non-continuous forest biomes, resources would have been reduced not only in their overall diversity, but also in their overall abundance and spatial distributions. Indeed, hominoids of this period would necessarily have had to adapt, behaviourally and morphologically, in accordance to the restrictions imposed by the evolving ecosystem. To some extent, such adaptations likely resulted in episodes of niche differentiation, and very possibly in extreme instances of niche exclusion and subsequent migration.

During the earliest part of the middle Miocene, species diversity appears to have decreased somewhat in conjunction with an apparent depletion in resources. As defined in Chapter Three, two key hominoid groups (i.e., the family Oreopithecidae and the genus

Afropithecus) are accounted for in the early Middle Miocene fossil records of east Africa. As Andrews *et al.* (1997) explain, the east African environments associated with these two groups were likely dominated by dry woodland to more densely-covered forested areas . However, these authours further explain that alternate evidence tends to suggest that, forest or no forest, resource availability would have been greatly impacted by increased levels of regional seasonality. While the number of hominoid species present in east Africa during this time span was fewer than the early Miocene, an apparent decrease in resource availability would have been a key source of competition and stress for even this small(er) number of species. In addition to these environmentally induced resource-stresses, resource availability would have been further reduced in light of a potential increase in competition as may have occurred with the appearance and seemingly rapid proliferation of cercopithecoids (i.e., *Victoriapithecus* and *Microcolobus*) within these same environments.

In response to ecological stress and the increased potential of intra and inter-specific competition, early middle Miocene hominoids in east Africa appear to have undergone extensive behavioural and morphological adaptations. All such adaptations definitely facilitated some degree of co-existence, on the part of both apes and monkeys, through niche differentiation. Early to mid Miocene cercopithecoids appear to have been semi-terrestrial quadrupeds expressing a fairly eclectic suite of morphologies and inferred behaviours. Those hominoids, contemporaneous to these monkeys, appear to have maintained a life in the trees in spite of the decreased availability and discontinuity (both in time and space) of arboreally stored resources. Consequently, arboreal hominoids of the earliest middle Miocene were likely able to avoid extreme competition with semi-terrestrial cercopithecoids. However, the potential for conflict and competition *among* hominoids would have remained a serious threat. Within the constraints of an arboreal life, morphological and behavioural adaptations would have ensured that any overlap of

and competition for niche space was kept to a minimum. Post-cranial evidence suggests that oreopithecids maneuvered the arboreal niches by means of scansorial climbing combined with frequent bouts of arm-swinging. What little dental evidence there is for African oreopithecids suggests that there was an increased tendency towards folivory among these species. In contrast to oreopithecids, *Afropithecus* appears to retain a morphology indicating the employment of a more primitive form of arboreal quadrupedalism, one most similar to earlier *Proconsul*. While a thickening of enamel on the molars hints that this hominoid might have been increasingly dependent on hard, tough skinned food items, the overall configuration of these afropithecine teeth gives greater support to the idea that these primates maintained a frugivorous diet. Whether eating ripe fruit, or harder foods, what is important in the dental and postcranial elements of *Afropithecus* is that this species would have been able to avoid, with relative success, excessive competition with both monkeys and other apes.

While niche exclusion among early middle Miocene hominoids, as outlined above, may have been the norm, there is evidence that levels of intra and inter-specific competition may have been of such a severe nature as to result in the complete niche exclusion, and utlimately the inter-continental migrations of some hominoid species. A well documented series of migration events, collectively referred to as the "Proboscidean Datum Event", are known to have occurred at approximately 17.5 Ma, if not as early 19 Ma (Thomas 1985; Tchernov 1992). These events coincide with a seemingly mass migration of many animal species, including primates species (principally, a pliopithecid-like primate group) out of Africa (Thomas 1985; Barry *et al.* 1986; Harrison *et al.* 1991; Tchernov 1992). The primary route of migration, from east Africa into Eurasia, was believed to have been facilitated by the docking of the Afro-Arabian plate and the subsequent formation of a land bridge between the two continents (Thomas 1985; Tchernov 1992; Whybrow 1992). As Figure 7b demonstrates, during the earliest

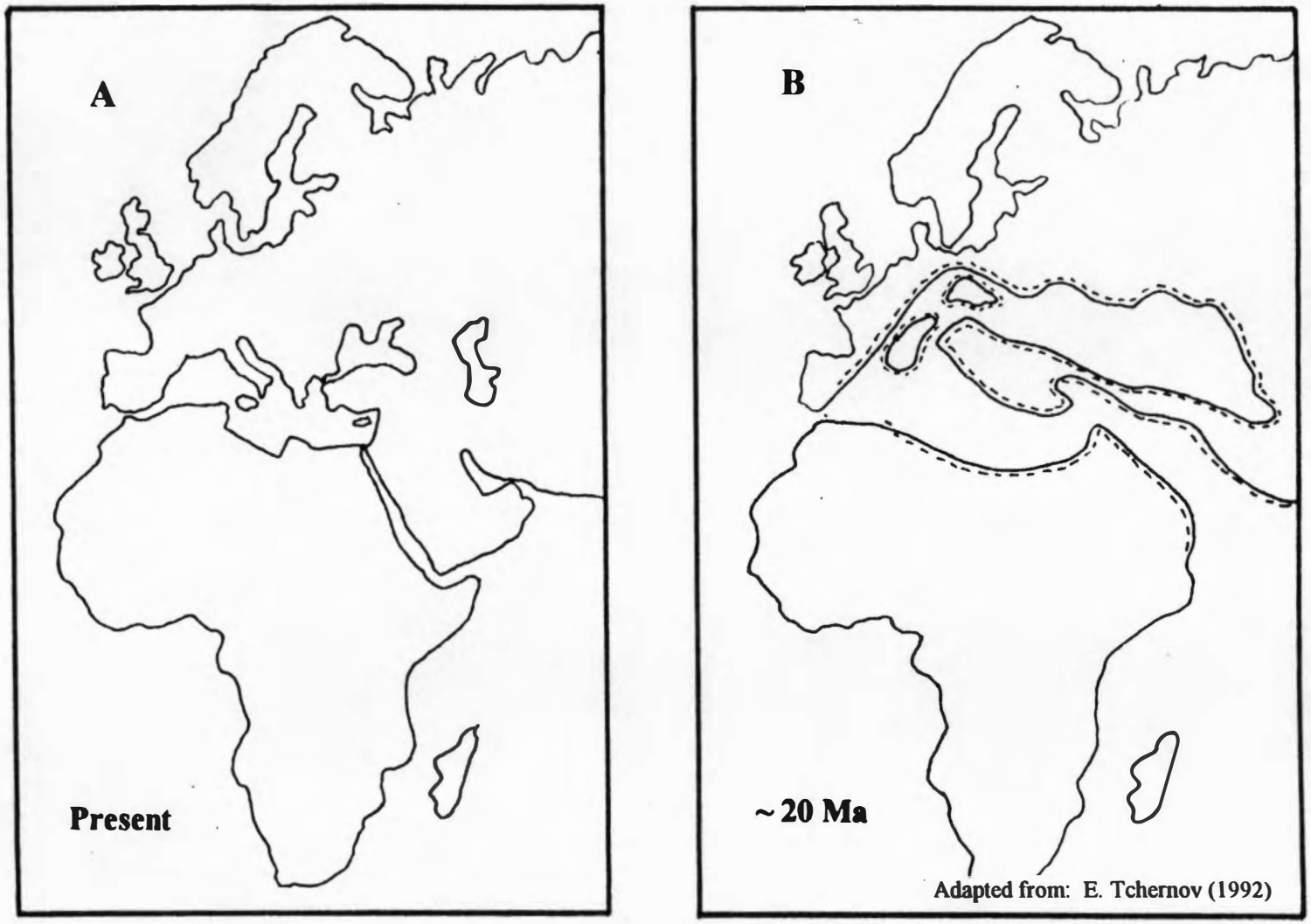


Figure 7. Configuration of the Circum-Mediterranean Regions of the Old World.
A = Present Configuration. B = Configuration at ~20 Ma.

Miocene, an expansion of the Tethys and Paratethys waterways left Africa and Eurasia virtually isolated from one another. However, by at least 18 Ma, a receding of these major bodies of water, in combination with the tectonic uplifting and bridging in the Arabian peninsula, opened up a vast corridor bridging east Africa (i.e., Ethiopia and Arabia) to areas of the Middle East (i.e., Iran) and western Europe (Harrison *et al.* 1991) (see Figure 8). It is by means of this bridge that the earliest hominoids are thought to have first dispersed out of Africa.

Of key importance to this discussion is the appearance of two hominoid genera (i.e., Pliopithecidae and *Heliopithecus*) out of Africa around this time. While completely different in their morphologies, both hominoid groups appear to represent successful, eurytypic hominoid species, each demonstrating morphological continuity/similarity with earlier African forms. Pliopithecidae in Europe, shows many morphological characteristics reminiscent of early Miocene *Dendropithecus*. However, in contrast to these possible African "ancestors", this hominoid evinces a appears more generalized/derived morphology. Postcranially, Pliopithecidae demonstrates a suite of characteristics which suggest of a greater reliance on quadrupedal *suspensory* activities. The dentition of pliopithecids indicates that these hominoids, compared to their putative ancestors, were much more eclectic in regards to their feeding behaviours and strategies. Together, both cranially and post-cranially derived generalizations would have afforded these apes the opportunity to exploit more wide-spread and varied resources. *Heliopithecus*, from Turkey, expresses many similarities to earlier afropithecines. Venturing into more arid and open terrains, the thick enamel of this apes teeth would have allowed *Heliopithecus* to exploit otherwise unaccessible food items. Together, both Pliopithecidae and *Heliopithecus* provide the first real indications of the hominoid trend towards morphological and behavioural generalization. Such a eury-typism would have

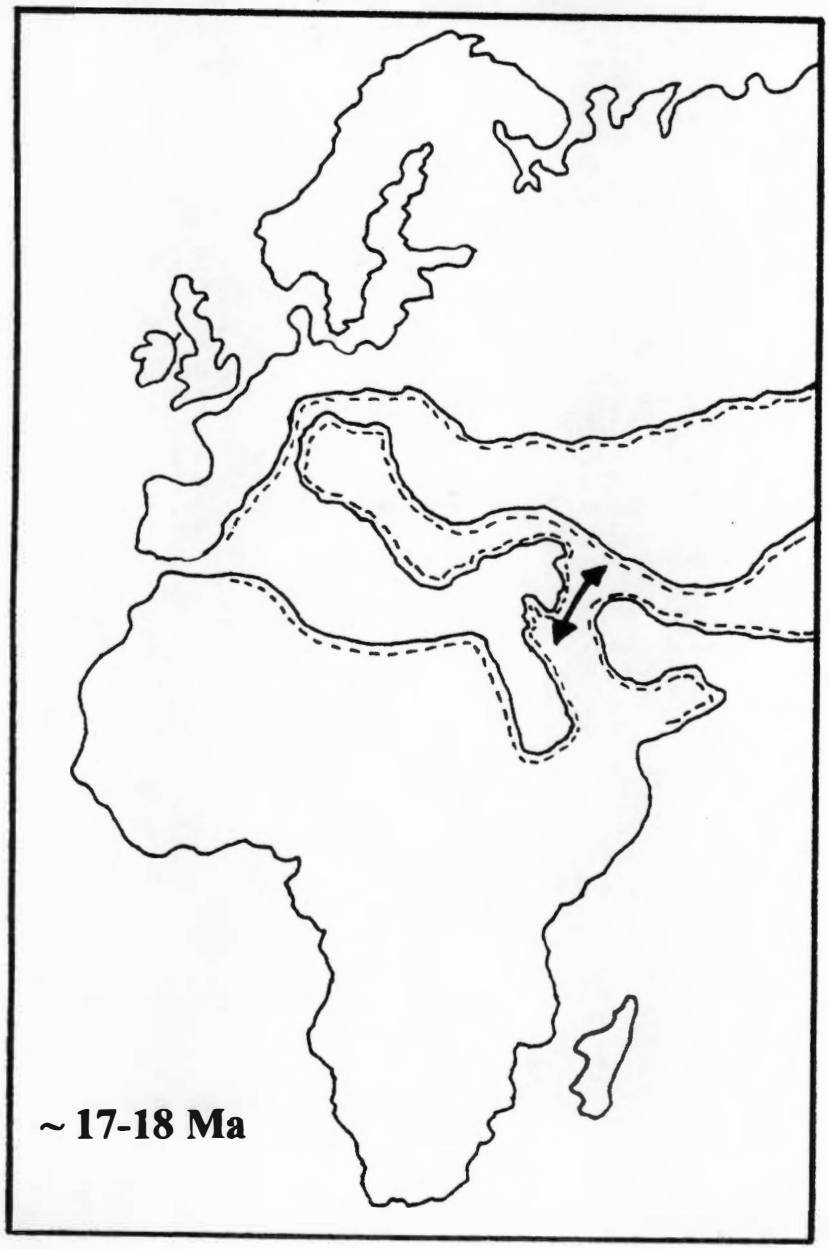


Figure 8. Configuration of the circum-Mediterranean regions of the Old World ~17-18 Ma (⎓ reconstructed regions).
Adapted from: H. Thomas (1985) and E. Tchernov (1992).

made possible: 1) a successful avoidance of competition among African apes and monkeys and 2) the subsequent migration into and successful adaptations within new and diverse environments.

Middle Miocene

As discussed in Chapter Two, the palaeoclimates and palaeoenvironments of the middle Miocene of east Africa were marked by events of significant cooling and drying. While the geographic relief of the middle Miocene (i.e., as affected by volcanism, plate tectonics and uplifting in the Eastern Rift Valley) was likely very dissimilar to the modern configuration (which did not appear until the late Miocene-Pliocene), there is little doubt that significant alterations in the topography had begun by this time (Boaz 1994; Andrews and Van Couvering 1975). Undoubtably, regional up-lift, while it may have been minimal, would have had repercussions on the regional climate systems and ecological contexts of evolving hominoids (Andrews and Van Couvering 1975; Malone 1987). The overall trend of the combined effects of global and regional climate change was towards more mosaic environments wherein tropical (C3) plants were increasingly being replaced by more resilient, dry-adapted (C4) plant species (Morgan *et al.* 1994; Cerling *et al.* 1991; Cerling *et al.* 1993; Kingston *et al.* 1994). Indeed, resource-rich patches invariably became fewer and farther between. As the diversity of resources dropped, so too did the diversity of hominoid primate species in east Africa. Only two hominoid genera are known to have persisted into the middle Miocene of east Africa, *Kenyapithecus* and *Otavipithecus*. As discussed in the previous chapter, the phylogenetic position of *Otavipithecus* in relation to all other hominoids is a great mystery. Based on the very primitive features associated with this ape's dental and postcranial remains, *Otavipithecus* is an anomaly whose regionally restricted success may have a great deal to do with its primitive retentions

and/or its geographical isolation (i.e., excessive niche differentiation). But more information is needed before any sure conclusions can be reached.

In contrast to *Otavipithecus*, *Kenyapithecus* is more fully understood. The environments associated with *Kenyapithecus* are comparably dry and open relative to earlier Miocene hominoid locales (see Chapter Three). Indeed, general ecological and climatic stresses would have seriously impacted the availability of an already reduced resource base. In addition, increased levels of competition associated with rapidly proliferating populations of cercopithecoids would have further aggravated resource availability. Previous arguments (i.e., McCrossin and Benefit 1994) have maintained that, for the most part, kenyapithecines lived in regions entirely separate from those occupied by contemporaneous cercopithecoids and, consequently, were subject to minimal competition with these monkeys. Further, these same authors support that, under those circumstances where monkeys and apes were in closer association with one another, differential feeding and locomotor behaviours would have been sufficient enough as to keep levels of competition at a minimum .

To date, the bulk of kenyapithecine evidence supports the notion that these early apes were, in fact, large, semi-terrestrial quadrupeds (McCrossin and Benefit 1993, 1997; Benefit and McCrossin 1995). The large body size of these hominoids would have necessitated that substantial quantities of possibly less nutritious food resources be acquired and consumed by these primates. Although the most recent discoveries (as discussed in Chapter Three) do provide intriguing indications of a more derived "hominid/hominoid" condition - a condition much different that the one outlined above - more fossil evidence and further study is needed to overrule what the earlier and more abundant evidence appears to support. For the purposes of this thesis, then, it will be maintained that middle Miocene hominoids were semi-terrestrial quadrupeds. Given that the post-cranial elements of this hominoid appear as strikingly similar to semi-terrestrial

cercopithecoids, it is doubtful that these two separate catarrhine groups could have existed completely isolated from one another.

While dental and cranial evidence may be employed as a means of supporting a lack of hominoid-cercopithecoid competition (i.e., McCrossin and Benefit 1994), it can also be used to reveal tendencies towards definite degrees of overlap in niche/resource exploitation. Dentally, evidence suggests that kenyapithecines, with their enlarged incisors and thick molar enamel, likely maintained a diet heavily reliant on tough food items such as seeds, nuts and unripe fruits. Given their large body size, a great quantity of such items would have needed to be consumed. In contrast to these hominoids, it is generally held that the dentition of Miocene monkeys retained more primitive catarrhine features, such a low crowned molars, and consequently would have relied heavily on ripe fruits. As such, the dietary requirements of monkeys compared to apes (i.e., ripe fruits for the former, harder foods for the latter) would have been different enough as to minimize levels of competition. However, evidence for incipient bilophodonty and incisal modifications among cercopithecoids suggest that they may have expressed increasing preferences for tougher skinned, unripe fruits. Such cercopithecoid developments would, then, have invariably placed these monkeys in more direct competition with coeval kenyapithecines. Although it cannot be substantiated (due to a lack of preserved evidence), any modifications in the cercopithecoid digestive tract would have further given the "competitive edge" to the proliferating cercopithecoids. Whether these morphological adaptations can be said to have existed, or whether they were responsible for the African demise of middle Miocene hominoidea remains to be seen. However, that conflict between monkeys and apes did play a definite role in the niche competition, niche differentiation and ultimate niche exclusion of middle Miocene hominoids cannot and should not be overlooked as a prime factor moderating hominoid adaptation, migration and evolution.

The African "Black Hole" and Implications of Taphonomic Bias

With the exception of a few kenyapithecine and a few other relatively indeterminate fossil remains, the hominoid fossil record becomes and *remains* fragmentary throughout the remainder of the Miocene (see Hill and Ward 1988; Hill 1994b for a review). It is not until the terminal Miocene-Pliocene boundary (~4.5 Ma) that one sees any conclusive evidence for hominoid or hominid ancestry and evolution within east Africa. Although there is no defined process or circumstance which can establish with absolute certainty the reasons behind the persistence of a fossil "Black Hole" throughout the mid to late Miocene of east Africa, certain notions of taphonomic and sampling bias may be said to provide some useful clues. Hill (1985; 1987) explains that discrepancies (or missing pieces) in the fossil records of east African sites likely have everything to do with factors relating to sampling. First, following Hill's logic, it may be that the overall representation (or lack thereof) of a certain taxon is only proportional to, and therefore limited by, the actual size (i.e., numbers) maintained by a population during its occupation of a given site or region. Hill further explains that the more rare or uncommon a species is during its history, the less likely it is that this species will be preserved in the fossil records. The body size, location and regional dispersal of hominoid taxa may also effect the preservation of a specimen. In fact, it has been determined that larger animals deposited in a non-lacustrine area tend to be less well preserved and represented in a fossil sample. This lack of representation may be further biased by the displacement and dispersal of specific groups *beyond* the boundaries of the site under study. Finally, as Hill also maintains, aspects of accurate chronology and restrictions in the quality and quantities of sites uncovered may also skew how one perceives and interprets the fossil records.

Indeed, a great many of the above sampling factors may be said to have contributed to the apparent "Black Hole" that appears in east Africa during the middle Miocene. In the case of kenyapithecines, from basic ecological principles (i.e., ecological setting and resource distribution as determinants of population sizes) it can be deduced that, in fact, the species diversities and population sizes were probably small for these hominoids. As such, the overall under-representation of these hominoids in the fossil records may be an artefact of the population structures of these primates. As large primates, it is fairly probable that kenyapithecines foraged greater distances as a means of: 1) escaping cercopithecoid resource competition, and 2) acquiring enough bulk and food energy so as to fulfil their dietary needs. In sum, the sheer size and the likelihood of kenyapithecine foraging dispersal may also have been of great import in relation to the degree of representation of these hominoids in the fossil records.

The above considerations of kenyapithecine preservation and taphonomic bias do lend support to the notion that the scarcity of middle Miocene fossil hominoids may not be entirely due to a disappearance of hominoids in Africa, but rather may be due to significant changes associated with populational densities, diversities, and dispersals. However, it must be kept in mind that much of east Africa, especially the Rift Valley, is extremely well studied and documented both spatially and chronologically (especially as relating to numerous volcanic sediments throughout the Rift System). In spite of the apparent means by which missing links can be accounted for (i.e., Hill's discussion), the fact remains that there exists an expansive measure of time (~10 million years) and space wherein African hominoids *have not* been found and therefore *cannot* be proven to have existed. Napier aptly explains one must always bear "...in mind the proviso that negative evidence proves nothing" (Napier 1969, p. 83). With no hard evidence for support, we can neither prove nor refute that hominoid lineages leading to hominid ancestors persisted in east Africa. Indeed, future evidence, if ever recovered, might substantiate either claim -

its a flip of the coin. Rather than sit idle and in-wait for any missing fossil links within east Africa, it is essential that alternative areas and avenues of hominoid evolution be explored.

In taking the focus off of the African continent, it becomes apparent that hominoid adaptation and evolution did continue throughout the middle Miocene and extended throughout other areas of the Old World. In fact, there is much evidence which can be used to support that kenyapithecines, in responding to extreme levels of stress induced by factors of the environment and competition, were likely the subjects of extreme niche exclusion and subsequent migration events out of Africa. As Figure 9 demonstrates, in spite of the re-expansion of the Tethys-Paratethys waterways, narrow corridors likely continued to bridge Africa to Eurasia between 14 and 15 Ma (Thomas 1985; Tchernov 1992). During this time, much of the Arabian peninsula (i.e., Lybia, Egypt, Israel and Saudi Arabia) was becoming increasingly more arid (Tchernov 1992). However, most migrant faunal assemblages, of which hominoids were invariably a part, showed an increased tolerance (i.e., morphological adaptations) for more open and dry environments (Tchernov 1992). In Turkey *Griphopithecus* appears at roughly this time. As discussed in the previous chapter, this large bodied, quadrupedal hominoid shows some similarities with *Kenyapithecus*. Such similarities do suggest that *Kenyapithecus* did, in fact, radiate out of Africa. Some time later (~ 13Ma), in Europe another hominoid *Austriacopithecus* appears in the fossil records. This species also expresses some affinities to earlier African kenyapithecines, and consequently, lends support to the notion that, while kenyapithecines may have disappeared from within the African continent, their adaptations and subsequent evolution facilitated a radiation of this ape over both time and space. Another hominoid migration event associated with the middle Miocene bridges over the Tethys is that of *Sivapithecus*. The significance of *Sivapithecus* in relation to later hominoid adaptation

Figure 9. Configuration of the circum-Mediterranean region of the Old World ~14-15 Ma (--- reconstructed regions).
Adapted from: H. Thomas (1985).

and evolution is unclear. However, of great importance in regards to this hominoid is its observed morphological trend towards a much more derived condition. For both sivapithecines and kenyapithecines out of Africa, as with earlier Miocene migrant primates (i.e., pliopithecids), the key to the survival and geographical and temporal tenacity was very likely linked to their increasing behavioural and morphological flexibility and generalization.

Middle to Late Miocene

In light of obvious climatic/environmental deterioration and increased levels of competition within Africa from the middle to the late Miocene, it can be logically deduced that Eurasia became the sanctuary/haven to which hominoids escaped and in which they further evolved. As already discussed in previous chapters, throughout much of the Miocene, the climatic conditions in Europe and Asia remained predominantly subtropical. Of course the biomass produced under such climatic/environmental conditions would have been somewhat less (both in terms of the kinds and numbers of plant resources produced) than the biomass produced in exclusively tropical environments. Consequently, the kinds and numbers of consumers able to exploit these resources would have been correspondingly low. Indeed, the diversity among European hominoid species appears to be fairly low with approximately only five genera represented over a span of nearly 7 Ma (i.e., *Paidopithex*, *Austriacopithecus*, *Dryopithecus*, *Ouranopithecus* and *Oreopithecus*). While there may have been some temporal overlap of these late Miocene European Hominoids, their wide spatial distribution (i.e., across Europe, from Spain to France to Austria to Germany to Hungary and finally to Greece) would have minimized the likelihood of intense competition among these apes. In addition, species-specific

morphological and behavioural adaptations would have further reduced instances of niche overlap and competition.

As Begun (1992a) clearly demonstrates, and as discussed in Chapter Three, locomotor behaviours among these European hominoids were quite dissimilar. *Paidopithex* morphology is indicative of a high degree of quick and agile quadrupedal suspension, much like the platyrrhine howler monkey. Begun (1992a) suggests that *Paidopithex* evolved *in situ* in Europe, most probably from some pliopithecid-like ancestor. In their arboreal environment, these hominoids likely experienced very little competition and, hence, were able to monopolize a monkey-like niche while retaining a more "primitive" dietary regime and locomotor repertoire. As mentioned already, *Austriacopithecus* expresses many similarities with earlier kenyapithecine hominoids. Of key note is this ape's morphological proclivity towards an exclusively quadrupedal (arboreal and/or terrestrial) mode of locomotion. These quadrupedal tendencies would have made niche overlap with those coeval suspensory hominoids very unlikely.

Species of dyropithecines appear to represent the least specialized, most eclectic/diverse post-crania of all the European hominoids. While there are hints that these apes continued to demonstrate some more primitive quadrupedal behaviours, the bulk of post cranial evidence suggests that increasingly these apes were becoming more reliant on suspensory-based locomotion. It may, in fact, be among these European dryopithecines that the first real glimpse of a highly derived, truly hominoid-like mode of forelimb dominated suspensory locomotion appears *outside* of Africa. As discussed in the previous chapter, the dentition of dryopithecines demonstrates that these apes, while they may have included some leaves and hard food items in their diet, were most reliant on soft fruit items. Given the increasingly larger body sizes of these hominoids, dryopithecines very likely would have needed to supplement fruit-based diets with large quantities of low quality foliage. However, the distinct morphological and behavioural differences of these

dryopithecines compared to other European hominoids would have reduced chances of niche overlap and direct competition, thereby ensuring (or at least increasing the likelihood) that adequate supplies of ripe fruits would have been more readily accessible for their consumption.

Ouranopithecus is one of the most spatially and ecologically distinct of the European primates. Its apparent isolation from other hominoids would have reduced, if not completely eliminated, levels of competition. As found exclusively in northern Greece, this hominoid appears to have inhabited one of the driest, most open regions of Europe during the latter portion of the Miocene. Although nothing has been recovered of its postcrania, cranio-dental evidence reveals that this was an extremely large primate. Such a large size would have made a completely arboreal existence difficult, if not altogether impossible. What cranio-dental evidence is available for *Ouranopithecus* (especially the thick enamelled, relatively large molars) strongly suggests that the diet of this hominoid was based on hard and course food items. Together, the inferred body size and dental configuration of these apes support that *Ouranopithecus* would have necessarily inhabited and exploited a terrestrial niche.

Finally, as found only in Italy, *Oreopithecus* appears to represent one of the most temporally distinct hominoids in Europe. Remains attributed to this ape have been dated to as recently as ~10-6 Ma . As discussed already, *Oreopithecus* is very enigmatic in regards to its relationship with other European (and African) hominoids. In its exploitation of very dense, humid pockets of swamp-like forest this ape engaged in a very derived, hominoid-like hindlimb dominated form of suspensory locomotion. Postcranially it retains markedly primitive catarrhine features. During the latter part of the Miocene, given the rapid decrease in hominoid species throughout Europe, it is apparent that the potential of niche and resource competition with other hominoids would have been very small . This, however, does not preclude that competition with other arboreal animals

(primate and non-primate) would have played a significant role in the adaptation and survival of *Oreopithecus.*

Late Miocene - Pliocene

Toward the close of the Miocene, the effects of major climatic perturbations were strongly felt both globally and regionally. On the African continent, a rapid expansion of the Saharan desert belt took place (Tchernov 1992). Meanwhile, eastern Africa was subject to a marked increase in aridity as aggravated by both global climatic cooling and regionally-based volcanism and doming (Tchernov 1992; Nakaya 1993, Ishida and Nakaya 1994; Boaz 1994). Although the replacement of forested regions by more open savanna biomes was not sudden or uniform in its occurrence, it was of very definite impact on the biotic composition of east African communities (see Chapter Two). As discussed, plants and animals alike were becoming increasingly more tolerant of arid conditions (Tchernov 1992). However, it appears that factors of environmental deterioration and increased levels of competition were enough to prompt waves of migration out of Africa among even the most arid-adapted fauna . It has been documented that as early as 9.5 Ma to 7.4 Ma (or the late Astracian to early Turolian), there was a significant, large-scale movement of taxa out of Africa (Barry 1985; Tchernov 1992). It is believed that such migration events continued until the terminal stages of the Miocene and likely culminated during the Messinian Crisis at around 5 Ma (Tchernov 1992).

As discussed in Chapter Three, during the late Miocene cercopithecoids were found throughout regions of northern and eastern Africa. Indeed it appears that behaviourally and morphologically, these monkeys were more similar to their extant descendants than earlier cercopithecoids (i.e., *Victoriapithecus* and Prohylobatidae).

Migrations of late Miocene monkeys out of Africa were known to have occurred via the Arabian peninsula (Barry 1985; Whybrow *et al.* 1990). However, as Figure 10 substantiates, a progressive drying out of the Mediterrean would have facilitated a large number of more direct migrations into Europe. Once in Europe these monkeys would invariably have come into direct contact with coeval hominoid populations.

From approximately 11 to 6 Ma, colobine-like cercopithecoids (i.e., *Mesopithecus*) are known to have existed throughout south and central Europe. The earliest species of *Mesopithecus* known to have migrated into Europe are those associated with fossil remains found at sites in Germany, France, Italy, Yugoslavia and the northern most reaches of Greece (Ardito and Mottura 1987). Each of these areas (as discussed in Chapter Three) has previously been shown to be key hominoid locales. Although, with the exception of northern Greek locales (see Koufos *et al*. 1991), no hominoids have yet been found in direct association with these Late Miocene monkeys, it cannot and should not be assumed that these two catarrhine groups did not come into contact with one another.

Indeed, instances of sampling bias (as previously discussed) may be contributing to a apparent lack of hominoid material at this time. As has been repeatedly discussed, European hominoids were comparably large. Recalling factors of sampling bias, it is known that larger specimens tend, on the whole, to preserve less frequently in the fossil records. Further, and in relation to the large size of these hominoids, it is known that the environmental/ecological conditions of Europe, while they were comparably lush, were no where near as resource-rich as the more tropical environments of earlier African hominoids. The larger sizes exhibited by these European hominoids, and their absolute energy requirements (as measured in larger quantities of likely less nutritive value) were likely such that the total numbers and kinds of species able to feed within a restricted range were necessarily few. As such, these hominoids may have been forced to live and

Figure 10. Configuration of the circum-Mediterranean regions of the Old World ~ 5-6 Ma (--- reconstructed regions).
Adapted from: E. Tchernov (1992).

forage in small, very dispersed units so as not to exceed the carrying capacities of their local and preferred niches. Such factors of population sizes and ranges of dispersal may then also be factors contributing to an apparent under-representation or complete absence of Late Miocene European hominoids in association with cercopithecoids.

If, then, one supports that cercopithecoids did encroach upon hominoid locales, it is necessary to reveal if and how such encroachment affected levels of niche competition. Within the northern regions of Europe, it is apparent that the climate and ecology remained fairly consistent throughout the Miocene (Ardito and Mottura 1987). However, it is apparent that the circum-Mediterranean regions became progressively more arid and open (Ardito and Mottura 1987; Koufos *et al.* 1991; Tchernov 1992). Some more northern-based hominoid and monkey groups (i.e., *Dryopithecus* and *Mesopithecus* in Germany) may have been able to maintain minimal levels of niche overlap and competition. Dryopithecines would have been able to monopolize the arboreal component of their shared environments while cercopithecoids dominated more terrestrial niches. By contrast, hominoids occupying the circum-Mediterranean regions of Europe, would have been forced into more intense and frequent bouts of competition. While certain elements of postcranial morphology do support that fact that some hominoids maintained a more or less arboreal way of life (i.e., *Dryopithcus* and *Oreopithecus*) and, therefore, were likely able to avoid direct competition with more semi-terrestrial cercopithecoids, dental and other evidence provides some clues which can be used to support the contrary (i.e., increased competition). Bilophodonty among these early cercopithecoids suggests that these monkeys were, to some extent folivorous. Given this, it may be suggested that these monkeys would have posed little threat to predominantly fruit-oriented hominoids. However, if one is to assume that these early cercopithecoids were approaching the distinction of a true cercopithecoid morphotype, it cannot be discounted that some characteristics of the gut morphology had already evolved among these primates. As

such, it must be taken into consideration that these monkeys, while they might have relied heavily on a diet of leaves, might also have incorporated a larger portion of hard skinned, semi-toxic, unripe fruits. The potential monopoly of these monkeys over unripe fruits would have obviously limited the amounts of ripe and digestible fruits available to arboreal hominoids. Similarly, terrestrial hominoids (i.e., *Ouranopithecus*) would have been doubly restricted. In an already resource-restricted area (as restricted by immediate factors of increased drying and subsequent niche reduction) *both* terrestrially and arboreally found food items would have been further reduced under added conditions of intra-specific competition.

Towards the later Miocene and earliest Pliocene, other groups of cercopithecoids are known to have invaded parts of Europe - *Dolichopithcus* and *Paradolichopithecus*. Such incursions would have seriously impacted hominoid abilities to maintain monopolies over their preferred niches. In addition to these migrant monkeys, it has also been suggested that a proliferation within Europe of squirrels, bats and bears (all frugivorous species) also likely added insult to injury (Kortlandt 1983). As with early and middle Miocene apes in Africa, one possible means by which late Miocene European hominoids could have escaped/avoided excessive levels of resource stress and competition would have been to migrate. A northward movement into regions still predominated by subtropical biomes may have been possible. However, already high levels of competition would have likely already saturated any available niches. In addition, continued global cooling throughout the Mio-Pliocene and into the Pleistocene would have made continued occupation of these regions increasingly less possible (Nagatoshi 1987). Any eastward migrations towards Asia would have been halted by the Alpine-Himalayan mountain ranges (Tchernov 1992). Given the above, a southward migration, back into Africa, may be the most conceivable. Evidence exists which supports that numerous faunal migrations did bring taxa back to east Africa from southern Europe, Eurasia and even northern Africa

(Nakaya 1993; Ishida and Nakaya 1994). In fact, it has been demonstrated that most of the incoming groups were adapted to open environments and corresponding conditions of intense aridity (Tchernov 1992; Nakaya 1993; Ishida and Nakaya1994). While a re-penetration of Africa over the extremely hot and arid Mediterranean basin and, by then, fully established Sahara Desert belt (Tchernov 1992) would have been difficult if not virtually impossible for European hominoids, alternate avenues of return may have been available in regions of the Middle East. As Figure 10 demonstrates two possible land bridges remained open during the Mio-Pliocene boundary.

Re-immigration into Africa on a circum-Mediterranean-Arabian route would have been difficult. Extreme conditions of aridity likely prevailed for much of this time (Tchernov 1992). However, an increased tolerance for arid and open conditions, combined with an increase in eclectic behaviours and generalized morphologies would have greatly facilitated the migration of hominoid groups. Towards the end of the brief Mediterranean Salinity Crisis (~6.5 to 5.5 Ma) a significant retreat of open habitats and the reappearance of more expansive and humid forested biomes would have made these regions much more hospitable and more easily traversed (Tchernov 1992).

A key point of re-entrance into Africa would have likely been at the southern most connection of the Afro-Arabian plates. To refer back to Figure 10, it can be seen that a fairly substantial land bridge, joining the Isthmus of Bab-el-Mandab to Ethiopia, existed during this period of hominoid migration (Napier 1969; Tchernov 1992). It is likely much more than a mere coincidence that the earliest true hominoid/hominid species to re-appear in Africa after a 10 million year long "Black Hole" are those which have been found in the regions of east Africa immediately to the south of this juncture. The temporal and regional backdrop into which the earliest, most probable hominoids/hominids reappear seems to strongly hint that the transition from hominoid to hominid more than likely

occurred in a place and under circumstances external to the mid to late Miocene "Black Hole" which enveloped east Africa.

While there exists no concrete evidence which can be employed to prove or disprove an African evolution and origin of early hominids, there similarly exists very little evidence which provides direct support for a Eurasian evolution or origin. However three important issues must be raised at this time. First, the time-span separating the latest European apes from the earliest hominoids/hominids to reappear in Africa is significantly less (~3-3.5 Ma) than that separating early African hominoids from later hominids (~10Ma). As such, temporal proximity may be of greater use/import to us in our efforts to better understand phylogenetic proximity and ancestry. Second, a re-invasion of European hominoids into Africa by means of a circum-Mediterranean-Arabian route would have likely come about in response to severe climatic shifts (and the subsequent increases of catarrhine competition as outlined in previous sections). Such climatic shifts resulted in the desiccation of much of the Mediterranean and Red Sea areas. A subsequent and rapid re-flooding of these regions invariably would have a definite impact in relation to matters of hominoid taphonomy. It may, in fact, be the case that much of the evidence documenting a migration from north to south and the transition from hominoid to hominid may have been inundated with resurgence of these bodies of water. Finally, it must be kept in mind, some of the most recent and most hominid-like specimens *are*, in fact, found in Europe.

To date it is argued that the two best European contenders for African hominid ancestry are *Ouranopithecus* and *Dryopithecus*. An increasing body of evidence within east Africa demonstrates that a tremendous amount of variability existed among the earliest putative hominids (see the review in Chapter Three, also Kappelman *et al.* 1996). On the one hand there exists evidence of an arboreal large bodied hominoid with comparably thin molar enamel (i.e., *A. ramidus*). On the other hand, there are a number of

finds which indicate a thicker enamelled, semi-arboreal/ semi-terrestrial primate (*A. afarensis*). In between there are a variety of finds demonstrating a mosaic of features (see Chapter Three). Future studies and a more substantial reference base might eventually reveal that the earliest African hominids did, in fact, stem from European ancestry. Further, such information may demonstrate that these earliest probable hominids are likely the end products of two successful migration events of hominoids back into Africa. The first event may have involved a hominoid well adapted to the open and arid conditions which invariably prevailed over its course of travel (i.e., a thick enamelled, terrestrially bound hominoid, much like *Ouranopithecus*). A second migration may have included a more arboreally adapted, thin-enamelled group of hominoids that was able to monopolize the humid, forested regions which redefined the earlier migration root (i.e., a hominid of Mediterranean origin similar to *Dryopithecus*). Such migrations may help to explain the increasing amount of variability observed among the earliest, putative African hominids. However, the hidden subplots underlying hominid origins, adaptations and evolution will only be made more clear once the all the missing links are placed before us.

General Summary and Concluding Remarks

As this thesis has developed, the interface between organisms and their environment is of tremendous complexity. The science of ecology seeks to explore and explain this complex and dynamic interface by means of a thorough investigation of all conceivable patterns and processes, factors and variables. Indeed, in espousing the ideas and principles of such varied sciences as biology, natural history, climatology, geography, biochemisty, physiology and behavioural science, this multi-dimensional approach affords this unique science great success and insight into such complex patterns and processes as they occur in nature. Much of what is revealed through ecological study is that which can be observed and measured within a spatially and temporally delimited area. Very often little attention is paid by the ecologist to the more long term (evolutionary) consequences borne of such an interface between organisms and their environments. Such long term consequences are fundamental to studies of palaeoanthropology. This thesis has sought to bring together the fundamental elements and ideas of both ecological and palaeoanthropological science. Of key importance to this study has been the introduction and development of the notion of Ecosystematics. Essentially, it is the ideas of Ecosystematics which may serve as a bridge between short term (ecological) and long term (evolutionary) processes inherent to adaptation and the survival of individuals and, ultimately, evolution of populations and species within their complex and ever-changing ecosystems. Hence, it is Ecosystematics which can help palaeoanthropologists to better understand the patterns and processes behind both the proximate mechanisms of adaptation and survival, and any subsequent, long term evolutionary trends among hominoids.

As discussed at the beginning of this thesis, Ecosystematics (as relating specifically to the processes of hominoid adaptation and evolution) may be conceived of as an on-going play wherein the dynamics of the plot, the setting and the participant players are familiar to the viewer/interpreter. By understanding certain guidelines by which most plays are structured, it becomes apparent how the plot and outcome of a particular play, specifically that of hominoid evolution, may have unfolded over evolutionary time. As developed in Chapters One and Two, the backdrop of hominoid evolution is best revealed through a detailed understanding of each of the basic stages of the Ecosystematic cycle. Chapters Three and Four have developed how the key primate players have functioned within and contributed to this Ecosystematic cycle.

Factors of Ecology Stages One to Three: The Ecosystematic cycle begins with climatic variability (Stage One). As discussed, in ecological terms, the ideal ecosystem is one wherein a delicate balance is maintained between organisms and their environment. Such an ideal ecosystem very likely existed at the time of initial hominoid emergence and development (i.e., late Oligocene to early Miocene). However, the fragility of even the most ideal ecosystems must always be recognized. Over the course of hominoid evolution, fluctuations in the ecosystem, as induced by climatic shifts (i.e., regionally, globally, geographically moderated), are known to have occurred repeatedly. Ultimately, such shifts/fluctuations were of definite consequence to the subsequent levels of the Ecosystematic process. With climatic deterioration invariably comes the reduction of biomass production (Stage Two). As such, smaller quantities of potential energy at the base of the trophic pyramid will significantly imbalance the energy flow within the ecosystem. Of course, the effects of resource reduction seriously and negatively impact the internal dynamics of the ecosystem, thereby heightening levels of internal competition (Stage Three).

Factors of Evolution Stages Four and Five: Over the course of primate, or more specifically hominoid evolution, ecological disruptions and imbalances (as manifest through decreased resource availability and increased competition) have repeatedly occurred. The outcome of such disruptions and imbalances has usually resulted in varying degrees of primate/hominoid adaptation (Stage Four). As has been brought up numerous times throughout this thesis, variability and diversity among species was most marked among early hominoids. Within a lush and tropical setting, such diversity would have been only minimally restricted. However, climatic shifts, the environmental trend towards increased aridity and desiccation, and ultimately reduced levels of resource availability would have altered the kinds and numbers of species able to coexist within an ever-restricted environment. While high levels of diversity among hominoids would likely have been of minimal advantage from a short term/species vantage, great diversity and variability at the individual/evolutionary level would have been key to evolutionary success (Stage Five). From within and outside of Africa, it appears that climatic and environmental deterioration may have provided the perfect stage and setting for the adaptations of and selection for more generalized, "eury" hominoid traits. Indeed, such traits (both behavioural and morphological) would have better assured hominoid survival by increasing these species' chances of avoiding/escaping excessive levels of competition for shared or similar niches and resources. Such avoidance/escape would have been facilitated by those morphological/behavioural alterations which best accommodated extreme degrees of niche differentiation and exclusion.

On Geography and Hominoid Evolution: Of great importance in relation to patterns and processes of hominoid evolution - especially as related to niche differentiation and exclusion - is defining and understanding the temporal and regional distributions of these primates. As developed in this thesis, much of primate/hominoid evolution and the Ecosystematic cycle has been guided by the dynamic influences of geographic variability.

Such geographic variability, in addition to the aforementioned ecological elements, can provide tremendous insight into the plot and character development of this hominoid "evolutionary play". Geographic change does have great effects on regional and global ecosystems (i.e., as manifest through climatic variability, resource availability and competition). As such, geographic variability directly effects Stage One through Three of the Ecosystematic cycle. In addition, however, fluctuations in geographic configurations are of tremendous and direct consequence to Stages Four (adaptive responses, i.e., niche differentiation and exclusion) and Five (evolutionary responses) of this cycle.

As discussed, geographic bridges and barricades very often serve to restrict or perpetuate migration events. Within the confines of Africa, it appears the changes in the regional topography served to create regional barricades for certain animals (i.e., the east vs. west of the Rift Valley System). Indeed, for those primate which persisted within Africa (i.e., Cercopithecoidea) what few inhabitable environments remained were likely not much more than circumscribed islands of exploitation (Malone 1987). Primate distribution and competition, both within and between these discrete islands, would have contributed to an numerous speciation events.

In contrast to the above discussion, over the course of hominoid evolution, the formation of bridges, as opposed to barricades, appears to hold the greatest significance in regards to these primates' patterns of migration, adaptation and evolution. As revealed in Chapter Four, episodes of global and regional environmental desiccation have contributed to the drying out of major bodies of water and the subsequent formation of a number of corridors between African and Eurasia. Each such bridge is postulated as having served to the migratory advantage of numerous hominoid groups. As the Miocene progressed, and as land bridges opened, hominoids were able to escape areas of excessive intra- and interspecific competition. In migrating to areas only slightly different from their native Africa (i.e., sub-tropical vs. tropical) these early hominoids likely underwent only minimal

change (behavioural or morphological) in relation to their adaptive responses. As typically only the most "eury"-typic species appear to have migrated, the generalized behaviours and morphologies of these primates would have made their spatial transition comparably simple. On the whole it appears that the earliest hominoids to migrate out of Africa were very similar to their putative African ancestors. However, the discrete spatial and temporal placement of each of the Eurasian hominoids into regional pockets, and the progressive trend in Eurasia towards increased environmental variability (i.e., in relation to climatic deterioration and resource reduction) appear to have contributed to a tremendous amount of *in situ* (allopatric) speciation among these Eurasian hominoids.

As outlined above, factors of behavioural and morphological variability as well as geographic variability all contribute to the turning full-circle of the Ecosystematic cycle (i.e., the continuation of the evolutionary process). Morphological and behavioural adaptations towards a more generalized and flexible condition have repeatedly allowed hominoids to overcome potentially high-risk, high-competition situations. In addition, geographic bridges have served as a means of escape from such situations (i.e., through migration). Consequently, both adaptation and migration (as allowing for niche differentiation and, ultimately, exclusion) have ensured the continued survival and, most importantly, adaptation and evolution of hominoids from within and outside the African continent.

Some Implications for Hominid Origins: Generally it is assumed that Africa is the Cradle of Man. Such an assumption is logically linked to the fact that the earliest true hominids have been found exclusively in eastern (and possibly southern) Africa. As has been developed in this thesis, a tremendous time span marked by ever-increasing environmental desiccation seems to correspond with an apparent "Black Hole" in the fossil records of east Africa. Such a "Black Hole" may in fact be an artefact of sampling and taphonomic bias (see Chapter Four). However, factors of climatic and environmental

desiccation, as well as of heightened levels of intra- and inter-specific competition within Africa during this key period of the supposed African hominoid to hominid transition strongly supports that these African ecosystems may not have been those most suited to hominoid/hominid evolution. A definite lack of positive evidence in support of *in situ* African hominid evolution seems to corroborate this. Further, an increasing body of evidence derived from outside the confines of Africa seems to indicate hominoid/hominid evolution would have been more likely to take place in areas far displaced from the "Cradle of Man" - namely in Eurasia. Of course, negative evidence proves nothing. Indeed, future finds might help to further entrench certain preconceptions, or conversely, may serve to reveal these conceptions as real *mis*conceptions. Until these definitive clues are unearthed, it is essential that all possibilities continue to be considered and that all regions continue to be explored for their fossil potential. As this study of Ecosystematics has shown, ecological/geographical fluctuations have repeatedly prompted numerous primate migrations out of Africa. Invariably, such factors have also contributed to a re-invasion of the African continent by many mammalian groups, of which hominoids/hominids could most certainly have been a part. In summary then, until future finds are found, it may be more apt and safe to refer to Africa as simply the "Cradle of Catarrhines".

To conclude, one of the fundamental tenets of ecological science and theory is recalled: "No organism can exist by itself without an environment" (Odum 1971, p. 8). Further and in keeping with the key ideas developed throughout this thesis, it might be safely concluded that, not only can an organism *not exist* without an environment, but further, it similarly *cannot adapt* or *evolve* without an environment. It is hoped that future efforts aimed at reconstructing the patterns and processes of hominoid/hominid evolution continue to recognize, draw from and elaborate upon the fundamental ideas of ecology. In some ways it may appear that the units of study of the ecologist and the

palaeoanthropologist are diametrically opposed (i.e., the former focussing on the tangible present and the latter squinting at the more obscure past). However, it must be kept in mind that in many ways the patterns of the past may be only slightly different from those of the present. Like a formula play, whose plot, setting and characters are in some ways fairly well known to us, we may interpret the past as a precursor to the present. A clear recognition and understanding of these formulaic trends and the dynamic interplay between aspects of ecology and evolution - the essence of Ecosystematics- can and will continue to provide palaeoanthropologists with a tremendous insight into and understanding of the patterns and processes of hominoid evolution.

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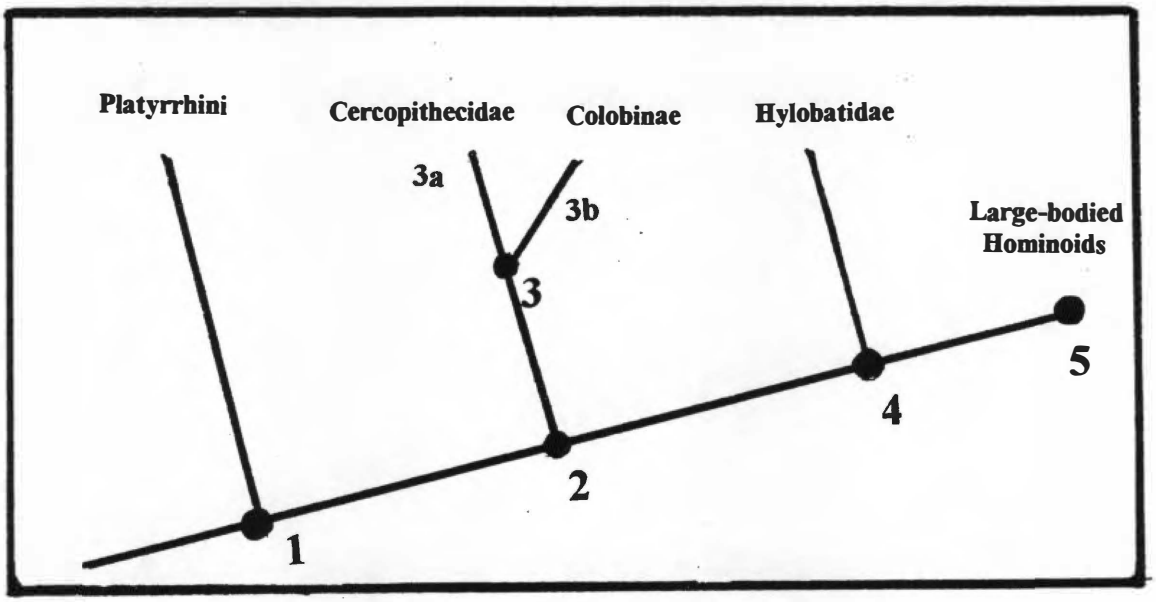
Appendices

Appendix A

Appendix A
List of Derived Catarrhine Features



Node 1

Ancestral Anthropoid Morphotype - Key Derived Features

(Sources: Andrews 1985b; Harrison 1987)

* premaxilla enlarged in incisor region
* facial region enlarged relative to neurocranium
* fusion of metopic suture early in development
* infraorbital foramen located on inferior margin of orbit
* fusion of the annular ectotympanic to the temporal bone
* enlargement of the promentory artery with an reduction/absence of the stapedial artery
* relatively complete separation of the orbits from the temporal bones by a (narrow) post orbital septum/pillar
* frontally directed orbits
* lacrimal bone contained *within* the orbital region
* fused mandibular symphysis
* high mandibular corpus with a reduction in the angular process
* bicuspid lower fourth premolar marked by subequal cusps, and large well demarcated mesial/distal fovae
* late eruption (i.e., after the replacement of the deciduous premolar) of the lower third molar
* a modified "hinge joint" of the pollex
* entepicondylar foramen present

Node 2

Ancestral (Extant)* Catarrhine Morphotype - Key Derived Features

(Sources: Andrews 1985b*; Harrison 1987)

* pronounced glabella as distinct from tori
* broader interorbital septum/pillar
* complete dissappearance of the lateral orbital fissures
* development of a tubular ectoympanic; tubular external auditory meatus
* loss of upper and lower second premolars; reduction in dental formula to 2-1-2-3
* laterally compressed, unicuspid lower third premolars
* honing surface on lower P3 for occlusion with the upper canines
* bicuspid lower fourth premolars, more long than broad
* heteromorphic cusps on all upper premolars
* maxillary molars all with 5 cusps and a small hypoconulid with M1<M2<M3
* lower molars with small hypoconulid with M3 slighly larger than M2 (i.e., M1<M2>M3)
* flat deltoid plane and narrow biccipital groove on humerus
* complete absence of entepicondylar foramen on distal humerus
* deep olecranon fossa on humerus
* saddle joint between carpals and metacarpals
* complete absense of the prehallux

Node 3

Ancestral Cercopithecoid Morphotype - Key Derived Features

(Sources: Andrews 1985b; Harrison 1987; Strasser and Delson 1987)

* loss of hypoconulid on lower P4 thru M2
* elongation of cheek teeth (i.e., narrow , "waisted")
* cusp realignment towards distinct bilophodonty condition
* extension of the lower P3 tooth flange well below the avleolar region creating an extensive honing surface for the upper canines
* extension/expansion of the canine groove down to the root
* parallel tooth rows in lower dentition
* fused mandibular symphysis with pronounced inferior transverse torus
* higher and extremely narrow nasal aperture (compared to the narrow, oval aperture primitve to anthropoids)
* medially placed mental foramen

* increasingly narrowed interorbital septum
* reduction in maxillary sinus
* stabilization of the ankle joint through modifications of the astragalar head and neck; limited capacities for the inversion of the foot
* modifications to the entocuneiform joint reducing range of adduction and abduction motions of the foot
* overall post-cranial modification accommodating greater motion, stability, agility of limbs in the sagittal plane

Node 3-A

Derived Cercopithecine Characters:

* extensive buccal pouch development (for food storage and early digestion)
* incisor specializations tending towards enlargement especially of the upper I2
* a reduction of enamel on the lower incisors contributing to the formation of self-sharpening, chisel-like teeth used for the cutting, scraping and overall preparation of fruits
* increased lengthening and narrowing of the nasal aperture
* longer, lower cranial vault
* mesial thickening of the mandibular corpus

Node 3-B

Derived Colobine Characters:

* modifications of the gut (i.e., sacculated stomach)
* extensive development of notches and cresting in the molar teeth
* thinner, blunt-edged incisors with moderately thick enamel as usefull for the gripping and tearing of leaves and other tough food items
* expansion in the gonial region of the mandible, with a thinning out mesially
* more slenderly built post-crania marked by longer limbs (as prerequisites for agility - running and leaping - in the forest canopy)
* reduction/loss of the external pollex and other modifications in the fore and hind limbs as associated with high levels of arboreal running and leaping (see Strasser and Delson 1987)

Node 4

Ancestral Hominoid Morphotype - Key Derived Features

(Sources: Andrews 1985b; Andrews and Martin 1987; Harrison 1987)

* enlarged paranasal sinuses
* breadth of upper I1 = height or upper I1
* low crown on lower P3
* reduced heteromorphy on upper premolars
* increased breadth of lower molars
* maxillary jugum development
* deepening of palate
* differential use of the forelimb over the hind limb
* upper limb modifications: lengthening of the clavicle; lenghtening of the mesial edge of scapula; large and rounded humeral head; medial orientation of the humeral head; pronounced trochlear keeling; shorten olecranon and reduced styloid processes of the ulna; broad sigmoid notch; bowing of the ulnar shaft; rounding of the radial head. In varying combinations these characteristics relate to distinctly hominoid functional complexes relating to:

    1) an increased capacity to lift forelimb above the head
    2) greater circumductionof the forelimb
    3) greater extension of the forelimb at the elbow
    4) greater wrist flexibility

* trunk and lower limb modifications: broad sternum; modifications of muscle attachments (origin and insertion points); modifications in vertebral column; reduction in lumbar vertebrae and loss of a tail; broader illiac blade;assymetry in femoral condyles; short, broad talus and calcaneus; distal portion of metacarpals increase in size/breadth. In varying combinations these characteristics relate to the distinctly hominoid functional complexes relating to:

    1) greater tendency for upright posture relating to locomotor and positional behaviours.
    2) greater flexibility and mobility (abduction, adduction and rotation) in the lower limbs

Node 5

Derived Characteristics of Large Bodied Hominoids (Great apes and humans):
(Sources: Andrews,1985b; Martin,1986; Andrews and Martin,1987; Harrison,1987)

Cranial modifications:

* marked mastoid process development
* larger maxillary sinuses
* orbit height>orbit breadth, with no overlap of the inferior orbital margin with nasal aperture
* long nasal bone
* increased aveolar prognathism with a marked lengthening of the premaxillary region
* junction of the maxilla and premaxilla marked by a "stepping" of the nasal chamber
* the incisive foramen small but "true"
* lengthening of the parietals in relation to the frontal

Dental modifications:

* upper I1 larger; I2 spatulate
* robust canines, with a decreased in P3 honing
* overall enlargement of the premolars
* upper premolars evidence less heteromorphy with a widening mesio-distally
* robust and broad lower P3s
* lower P4 lengthens with talonid height equal/proportional to trigonid height
* increased (although not necessarily uniform among all extinct or extant apes) thickening of molar enamel
* upper molars have an enlarged hypocone with reduced cingulum
* upper M1<M2>M3, M2 slightly longer than M1
* tooth rows wide apart anteriorly but basically parallel
* robust mandible with deep symphysis
* "low riding" inferiour torus > superior torus
* thick and robust mandibular corpus

Post-cranial modifications:

* reduction of ulnar styloid process with no carpal articulation
* coronoid process much higher than olecranon process of ulna
* strong keeling of the sigmoid notch

* deep sulci on either side of the lateral trochlea with pronounced keeling of humerus
* reorganization of the forelimb musculature (see Martin 1986; Andrews 1985)
* complete loss of ischial tuberosities
* hindlimb proportions decrease in relation to forelimbs (= high intermembral index)

Appendix B

Appendix B
Epoch Conversion Chart

Time M.A.	EPOCH	European Land Mammal Ages	Neogene Mammal Unit MN
1	Pleistocene	Steinheimian Bilharian Villafranchian Villanyan	MN17
2			
3	Pliocene		MN16
4		Ruscinian	MN15
5			MN14
6	late Miocene	Turolian	MN13
7			MN12b
8			MN12a
9			MN11
10	middle Miocene	Vallesian	MN10
11			MN9
12			MN8
13		Astaracian	MN7
14	early Miocene		MN6
15			MN5
16		Orleanian	
17			MN4
18			MN3b
19			MN3a
20			
21		Agenian	MN2
22			

Vita

Clare Katharine Stott was born on February 25, 1970 in Kalamazoo, Michigan. At the age of 5 she moved with her family to Edmonton, Alberta, Canada. Here, she was a student of the Edmonton Public School Board System. After graduating from Harry Ainlay Composite High School in 1988, she attended the University of Alberta, Edmonton. At the U. of A., Clare was enrolled in the Bachelor of Arts program, with a major concentration in Anthropology and a minor in French Language and Literature. In 1993 she received her Bachelor of Arts degree with honours-standing. Clare moved to Knoxville in 1994 to participate in the Masters' program offered through the Department of Anthropology at the University of Tennessee. Upon full completion of her Master of Arts degree, Clare will be attending the University of New Mexico to earn a Doctorate of Philosophy in Anthropology. Ultimately, Clare intends to teach Anthropology at the post-secondary level.