CONTINUITY OR REPLACEMENT:

THE ORIGIN OF MODERN HUMANS IN SOUTHEAST ASIA AND AUSTRALIA

by

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ABSTRACT

Two opposing theories have been expressed by researchers advancing descriptive models for the evolution and distribution of modern humans. The Replacement Model utilizes genetic and chronometric data, while the Continuity Model utilizes regional traits observed in archaic and modern populations within Southeast Asia and Australia. This evidence is analyzed and critiqued from a multi-disciplinary perspective which examines data from archaeology, paleo-ecology, zoology, geology, human anatomy, genetics, evolutionary theory and taxonomic classification systems.

It is concluded that although the Continuity Model appears to offer the more likely scenario, both models suffer from inadequate data and inherent problems in their underlying assumptions. Questions abound regarding problematic lithic typologies, doubtful depositional sequences, out-dated faunal correlations and flawed genetic-distance data. In addition, attempts to resolve this issue remain ambiguous within a taxonomic classification system that provides inadequate definitions for fossil species differentiation.

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INTRODUCTION

The Replacement Model and the Continuity Model are two opposing theories expressed by researchers attempting to explain the evolution and distribution of modern humans. The Replacement Model states that anatomically modern humans originated in a geographically restricted area and spread throughout the Old World, replacing all existing indigenous archaic populations in Europe, Africa, and Asia. This theory has received its most recent support from genetic mitochondrial DNA (mtDNA) data which identifies an African and non-African split, and suggests that all modern humans are descendants of a single woman who lived in Africa 200,000 years ago. Central to this model is the prediction that transitional forms of relatively great antiquity should be apparent solely in Africa. Associated with the transition should be the presence of modern regional characteristics in Africa but not in other geographic locations.

In contrast, the Continuity Model argues that *insitu* evolution from *Homo erectus* to modern humans occurred without replacement. This argument involves an initial radiation of *Homo erectus* from Africa during the middle Pleistocene, followed by gradual regional evolution within several areas including Africa, Europe and Asia. Researchers who support this model suggest that periodic gene flow between the peripheries of these geographic areas would prevent speciation; nonetheless, the regions were sufficiently isolated during the middle and upper Pleistocene to allow for the development and maintenance of distinct regional morphological features. Thus, paleontological indications of continuity, particularly transitional fossils and regionally distinct features, would link archaic and modern humans in specific geographic regions.

The purpose of my thesis is to test the validity of these two models by synthesizing, analyzing and criticizing formerly dispersed data from a wide variety of separate disciplines including archaeology, zoology, geology, paleo-ecology, evolutionary theory, human anatomy, genetics, and taxonomy in order to focus attention on the need for a multidisciplinary approach to the question of human origins. Unfortunately, this question has been discussed within the literature by specialists who argumentatively defend their data within the confines of their specific discipline and theoretical perspective. In fact, the origin of modern humans is a highly convulted question that cannot be answered by one particular discipline. Only by a concerted effort to amalgamate a wide variety of different types of analyses is it remotely possible to understand the relationship of inter-related variables involved in this evolutionary process.

I have researched the literature from a variety of disciplines and based my analyses on a series of six questions.

Question 1. Was there technolgical continuity or replacement in a peripheral geographic region such as China and Indonesia during the Late to Middle Pleistocene?

Question 2. Did paleoecological factors prevent or contribute to faunal and hominid migrations into China, Indonesia and Australia?

Question 3. Is there clear evidence for morphological continuity or replacement within and between Chinese, Indonesian and Australian fossils?

Question 4. How reliable is the context and dating evidence for the earliest anatomically modern human sites?

Question 5. How valid are the assumptions used by mtDNA research to suggest replacement of archaic humans on a worldwide scale?

Question 6. How do we recognize species in the fossil record?

I discuss these six questions by dividing the thesis into Part One and Part Two. In Part One, I critique the Continuity Model and focus on the technological, faunal, geological and paleontological evidence pertaining to the Lower and Middle Pleistocene of Southeast Asia and the Late

Pleistocene of Australia.

In Part Two, I critique the Replacement Model by analyzing the genetic data and the chronometric evidence from Late Pleistocene sites in South Africa that have been used to support the "Eve" hypothesis. Furthermore, I discuss the limitations of taxonomic analysis that have been used by both models and the inherent problems within classification systems that provide inadequate definitions for fossil species designation. Finally, I discuss the future potential of genetic analyses in providing further elaboration for questions regarding human origins, migrations and population affinities throughout the world.

PART ONE - THE CONTINUITY MODEL

CHAPTER ONE. HISTORICAL BACKGROUND

The roots of the continuity model are traceable to the unilineal schemes proposed by Hrdlicka after the turn of the century. His "Neandertal phase" model claimed that European Neandertals represented an ancestral stage in the phylogeny of modern humans. This model was formulated at a time when theories of human evolution were characterized by a distinct Eurocentrism (Smith et al. 1989, Spencer 1984). This viewpoint was understandable, considering it was based on the relative paucity of fossils from regions outside of Europe. However, as the fossil record expanded in East Asia, Chinese sites began to provide the most important support for the idea of gradual human evolution. During the 1940's Franz Weidenreich (1940, 1943, 1947) compared the morphology of Middle and Late Pleistocene Chinese fossils, and posited his polycentric views of modern human emergence whereby he envisioned many centres of origin with gradual evolution from archaic to modern humans. His Polyphyletic Model included parallel lineages in various regions evolving through separate Neandertaloid stages to the modern geographical variances of *Homo sapiens*. While he was unable to explain a mechanism for his evolutionary sequence, he suggested that the precursor species had evolved en masse into modern humanity through several morphological grades: from pithecanthropine (ape-man), to Neanderthal, to archaic, and finally into a modern grade. He states, "All facts so far available indicate that man branched off as a unit (from the ape line) which split afterwards, within its already limited faculties into several lines...I regard all the hominids, living mankind included, as members of one species" (Weidenreich 1949:157). Following his analysis of all the southeast Asian hominid fossils in 1943, he suggested that regional evolution of *Homo erectus* occurred in several world areas, resulting in the development of several major continental "races" of modern humans. He also suggested that osteological details of several prehistoric and recent Australian Aboriginal crania are evidence of a continuous line of evolution from the Javanese and Chinese fossils (Weidenreich 1946). For example, he proposed features that demonstrated a link between *Sinanthropus pekinensis* (Chinese *Homo erectus*) and modern Mongoloids, and between *Pithecanthropus soloensis* (Javanese *Homo erectus*) and modern Australian Aborigines. While recognizing that environmental factors in different geographical areas could result in regional differentiations, he believed these populations had not evolved in total genetic isolation and suggested there were varying degrees of gene flow between adjacent lineages.

Coon (1962) supported Weidenreich's hypothesis and extended the continuity concept to Africa and Europe, as well as Southeast Asian populations. He stated that Southern China, southeast Asia and the Indonesian islands constitute the homeland of the Australoid subspecies. However, his explanation for a polyphyletic model involved separate geographic subspecies evolving at different rates through time, thereby implying separate evolutionary rates and differently timed crossings of species thresholds. Coon's hypothesis argued that only genetic isolation could account for the development and maintenance of regional differentiation. He suggested that the degree of genetic continuity within each region over time greatly exceeded the degree of genetic flow between regions. "The races of man differ more from each other in a quantitative genetic sense than *Homo erectus* and *Homo sapiens* did, and our races are older than our species" (Coon 1962:37). However, Coon's argument does not explain how these regions could remain sufficiently isolated to produce regional selective differences without resulting in new speciation events.

Later researchers (Aigner (1976), Chang (1977), Thorne and Wolpoff (1981), Shutler (1984), Wu (1986), Smith (1984, 1992), Wolpoff et al.(1984, 1988, 1989), Pope (1991) and Wolpoff (1992) continue to follow Weidenreich's hypothesis and have consistently adhered to a scheme emphasizing technological, faunal and morphological continuity in China, Indonesia, and Australia.

In Chapters Two - Five , I discuss the technological, faunal, geological and morphological evidence in Southeast Asia for hominid replacement or continuity.

CHAPTER TWO. EVIDENCE FOR TECHNOLOGICAL CONTINUITY

2.1 China

Many Chinese researchers believe that cultural development during the Early Palaeolithic in China was a slow, gradual process beginning approximately one million years ago (Zhang 1985, Xinzhi 1985, Wu and Lin 1985, Wu and Dong 1985, Jia 1980, Aigner 1978). They have found that tools during this time period vary greatly in morphology and typologically classifiable tools are relatively scarce. Tools that appear to be multifunctional occur frequently and techniques of production are relatively simple. That is, flakes were made by four principle methods: simple direct percussion, anvil-supported direct percussion (bipolar technique), anvil (block-on-block) and throwing. Three major retouching techniques were employed, the most common being simple direct percussion. The bipolar and block-on-block methods were also occasionally utilized in the production of implements; however these fabrication techniques never account for more than a small percentage of the total artifacts in any given assemblage (Zhang 1985, Wu and Lin 1985).

Early Palaeolithic tools may be subdivided into two discrete categories. The first group includes tools used in the production of primary flakes and for retouching - principally hammerstones and anvils. Many of these implements are fashioned from pebbles or large cobbles that bear traces of battering and other use damage. The second category comprises finished tools such as scrapers, points, choppers, gravers, awls and stone spheroids. Most of these artifacts are made on flakes of various sizes and shapes, outnumbering core tools in Early Palaeolithic assemblages. Usually choppers are made from exhausted cores or pebbles, while choppers fashioned on large flakes are rare. Stone spheroids occur as core tools, while small implements such as scrapers and points are usually chipped on flakes. Thus, the early Palaeolithic traditions of China can be characterized as flake industries (Zhang 1985).

The characteristics of the Chinese Early Palaeolithic industries distinguished them from contemporary traditions elsewhere in the Old World. While choppers and some large bifacially flaked implements are known to occur, the Chinese Early Palaeolithic is not typified by the handaxes and cleavers so common in Acheulean industries of the western Old World (Aigner 1978). Many tool types and methods of fabrication first detected in the *Homo erectus* strata at the site of Zhoukoudien persist into Middle and Late Palaeolithic contexts in China. The bipolar technique, in particular, occurs in the archaeological record up through the close of the Pleistocene. The technological competence with which this approach to stone-working was executed underwent considerable progress as well (Aigner 1978).

Although cultural development was very slow during the Early Palaeolithic, Chinese prehistorians now have sufficient data to detect change within this immense time period.

Specifically, they observe the origin, fluoresence and eventual abandonment of the anvil method of flake production, while simple direct percussion continued to develop. Flakes and nuclei gradually became more regularized through time, as did the hammers used to produce them. Beginning with the simple natural elongated pebbles, hominids began to use more specialized strikers and finally batons of bone and wood for the production of more regularized flakes. Flake tools increase dramatically (in number) in relation to core tools during the Early Palaeolithic while tool types also increase in variety and regularity (Jia 1980).

Specific implement types may be seen to have undergone diachronic change also. Scrapers, for example, tend to become smaller through time and to exhibit increasingly regular, finely retouched margins. The absolute number of points associated with any particular assemblage also increased and they gradually became more refined. Choppers seem to have followed an opposite course of development in that they became demonstrably less sophisticated throughout the Early Palaeolithic and the absolute number also decreased. Presumably this is a result of their eclipse by smaller, more efficient task-specific implements (Jia 1980).

Simple direct percussion persists through the Palaeolithic as the principal means of retouching artifacts, although some of the specific techniques employed, such as alternating retouch, disappear from most later Palaeolithic contexts. The modification of flakes in general becomes more efficient through time and tools exhibiting a symmetrical plan form, shallow flake scars and regular edges eventually dominate the collections (Zhang 1985).

Several Chinese researchers have concluded the evidence for gradual *in situ* technological transition reflects continuity in the region and an absence of outside cultural influences from the West (Zhang 1985, Wu and Olsen 1985, Aigner 1978). At the same time, they suggest the north and south Chinese technocomplexes generally show affinites to Indonesia, such as the Javanese Pacitanean Industry, but do not show similarities to industries from Siberia, Europe, West Asia or Africa. However, recent researchers have negated this hypothesis. The issues surrounding this controversy are discussed in the following section.

2.2. Indonesia - the Javanese Pacitanean Industry

Questions regarding the tools used by the earliest hominids in Indonesia have been the subject of controversy since Dubois' work in 1891. In 1936 Koenigswald was one of the first researchers to find tools in the riverbed and terraces of the Baksoko River, which is located near the village of Pacitan, along the southeast coast of Java

The Baksoka River flows through the Zuider Mountains which are part of an uplifted limestone area (*Gunung Sewu*) called "Thousand Mountains" along the southeast coast of Java. The upper region of the Baksoka River lies in volcanic, clastic deposits, while the lower river region is situated in numerous, beehive-shaped cone karst mountains (Bartstra 1978). Karst topography results from the dissolution of carbonate bedrock and consists primarily of closely spaced sinks of large open-air solution cavities. This landscape is characterized by numerous, sinusoidal eroded limestone hills. Among these hills there are narrow, bowl-shaped valleys, in which lakes form during the wet monsoon season (Bartstra 1978).

Several terrace levels occur above the present bed of the Baksoka River. All the terraces are typical erosion levels of fluviatile deposit consisting of a base boulder gravel covered with a thin layer of red earth. The red earth is associated with a marked unconformity on the Tertiary sediments. The limestone hills rest on a volcanic formation, which includes shales and tuffaceous beds, containing layers of silicified tuff. In the base of the valley, where the volcanic series is exposed, large pebbles of silicified material occur in the riverbed (Movius 1948:352)

Koenigswald (1936) discerned two main river terraces at ten and twenty meters above the riverbed, but artifacts were found only in the river bed and along the ten meter terrace. He described these stone implements, found near the town of Pacitan, (Pacitanean) and identified many of the tools as "true" handaxes, similar to the Acheulean type from Europe and Africa. He proposed that because handaxes were present in the collection, the implements had to date from the early Pleistocene, thereby suggesting an association with *Homo erectus* (Koenigswald 1936:29).

By 1936, Koenigswald had collected a total of 2,419 artifacts; the majority of them were manufactured from silicified tuff. Movius (1944,1948) formulated an analysis of this collection and found that over 50% of the artifacts were made from flakes while the remaining tools consisted mainly of pebbles. Within the latter type of implement, choppers were the most common at 18% of the total, whereas handaxes were 6% of the total assemblage. Movius (1948:350-358) categorized these artifacts into five classes of major diagnostic tool types:

1. Chopping tools - These are core implements usually made on pebbles, or rough, tabular chunks of silicified rock. They are bifacially worked by alternate flaking exhibited by the intersection of alternate flake scars.
2. Handadzes - The secondary working along the edge is restricted to the upper surface of one end of these roughly tabular chopping or cutting implements. Preparation of this type produces the characteristic single-beveled, adze-type of cutting edge, in contrast to the double-beveled axe-type of cutting edge. These tools are usually made on cores, and the cutting edge, which may be straight, slightly rounded, or even pointed, forms a right angle with the long axis of the tool. They may be regarded as a special class of square or

rectangular chopper, rather than of round or oval form.

3. Proto-handaxe - Crude, roughly pointed or oval types of handadzes of plano-convex section are included in this category. They are worked only on the upper surface and are often made on flakes. The upper surface is flaked overall and the butt-end usually exhibits large areas of cortex. These tools appear to be transitional between handadzes and true bifacial handaxes.

4. Choppers and/or scrapers - The only essential difference between a chopper and a scraper is one of size. Both are unifacially flaked by secondary retouch on the upper surface. This type of tool usually has a round, semi-oval or almost straight cutting edge, formed by the removal of flakes from the upper surface of the tool. The cutting edge may be either along the side or across the end of the specimen. Although many of these artifacts are core tools made either on pebbles or angular chunks of rock, examples manufactured from large flakes are also common. A scraper is considered to be a small chopper and is usually made on flakes, but since the only criterion is size, no rule can be made to differentiate between scrapers and choppers.

5. Handaxes - One of the distinguishing features of this category is the longitudinal flaking parallel to the main axis of the tools. In contrast, handaxes of the Acheulean industries of Europe and Africa are flaked transversely to their long axis.

In addition, other minor classes include flake implements, utilized trimming flakes and cores. Movius (1944:91) stated that in the Pacitanian assemblage "the overwhelming majority...are made on flakes...strictly speaking, only a very small proportion...are true core tools." He admitted the subjectivity of his classification, stating "all categories are entirely arbitrary and the various classes...grade into one another almost imperceptibly (Movius 1948:350). His typological classification was based on morphology, while each implement class was "a purely artificial category" (Movius 1944:10,92).

Using the Javanese evidence, Movius made systemic comparisons between the artifact assemblages in East and South Asia. He suggested correlations between the geological and paleontological sequences and archeological assemblages from five culture areas: the Soan culture of northwest India, the Zhoukoudienian culture of north China, the Anyathian culture of Burma, the Pacitanean of Java and the Tampanian of Malaya.

Shutler and Forgie (1990) argue against Movius' use of culture areas and state that the "Tampan Culture" of Malaya became established in the literature over thirty years ago without the proper scientific scrutiny that would be accorded such claims today. Following Shutler's analysis of the material, he argues that the Tampanian assemblage does not consist of artifacts, but only broken rocks. At the present indicates that the Malay Peninsula does not have an Early or Middle Pleistocene culture, but apparently does have a Late Pleistocene industry (Shutler and Forgie 1990).

Yi and Clark (1983) have also contested Movius' categorization into a single tradition because it ignores the regional variations, complexity and diversity of lithic assemblages in each area. Although it is possible that these tools were manufactured by *Homo erectus*, it is only at Zhoukoudien that the correlation is conclusive. The other Southeast Asian assemblages have been randomly collected without reference to geological context and may date to the Upper Pleistocene or even the Holocene (Yi and Clark 1983).

Movius (1948) also made a comparison with the Lower Paleolithic of Europe and Africa and saw technological differences in lithic traditions. That is, India, Western Asia, Europe and Africa were characterised by the presence of handaxes (Chellean-Acheulean handaxe tradition), while South-East Asia, China and Indonesia were characterised by the absence of true handaxes and by the use of pebble tools (chopper/chopping tool tradition). According to Movius the difference between the lithic assemblages of the chopper/chopping tool culture area and the handaxe culture area are determined by two factors. First, the availability of raw material was sufficient to manufacture handaxes in the West, but was inadequate to do so in the East. Secondly, he suggested the lithic differences were due to ethnic differences i.e. differing cognitive systems that produced distinctive modal forms for tools with similar general purposes. However, Bordes (1968) states that raw material characteristics do not overwhelmingly determine tool shape and ethnic differences could not have been persistent over such enormous areas and time ranges that they produced entirely different assemblage types. Despite this criticism, Movius (1978) continued to adhere to his view, suggesting that "limitations and influences imposed upon the tools by the raw material from which they were manufactured are very great" (Movius 1978:352). Yi and Clark (1983) suggest the dichotomy of presence/absence of "typical handaxes" may be inadequate criteria for the definition of culture areas and for the assignment of a given lithic industry to a given tradition. In addition, the discovery of these handaxes in China, Malaya and Korea indicate this dichotomy is inconclusive.

In his initial analysis, Movius (1948) also states the rate of cultural progress in the east was relatively slower than in the west. He assumed that the trend of technological development in the Far East would follow the European trend from core-tool industries to flake-tool industries, to blade-tool industries and eventually to microlithic industries. However, the Eastern chopper/chopping tool tradition persists throughout the Pleistocene with minimal technological evolution. This view, that the Southeast Asian pebble and flake industries are not culturally progressive, remains in question. Yi and Clark (1983) indicate there is no reason to expect Asia (or any other area) to have followed the same developmental trajectory as other parts of the world. It is also possible that these tools are part of a 'maintenance' category, whereby they were used for manufacturing and sharpening task-specific wooden tools of (unpreserved) organic materials such as bamboo. Although the tools appear simple, amorphous and undifferentiated to a Euro-centric observer, the tools would have functioned at a sufficient level of efficiency.

However, Pope (1982, 1983, 1988) disagrees with this hypothesis and has formulated a Bamboo model within the karst environment, whereby a correlation exists between the geographic location of the chopper-chopping tool tradition throughout Southeast Asia with the location of verdant forests of bamboo throughout the same geographic area. The use of a specialized, non-lithic bamboo technology with wide-ranging functional types would negate the idea of a relatively slow rate of cultural progress in the East.

Following Movius' work in the 1940's, Van Heekeren (1972) continued work on the Pacitanian assemblage and adapted Movius' terminology in his analysis of 463 items from his own collection. He also found over 110 artifacts made from silicified limestone on the surface of the highest Baksoko terrace. His classificatory tables are directly comparable with the Movius analysis, with core tools appearing relatively unimportant, while flake tools are in the majority. Although Movuis and van Heekeren demonstrate the importance of a flake component in the Pacitanean assemblage, their terminology seems to obscure this fact because in their publications, core tools are more frequently illustrated than flake tools. When Mulvaney (1970) examined the collection he was surprised by the number, variety and size of the flake tools, since he had envisaged a core tool industry. While it is evident that these features were recognised by Movius (1944:92-93), Mulvaney believes they were not sufficiently emphasized and require further analysis. He suggests that the form was not important to the tool-users; instead, the specific edge (straight, convex, or concave) with a specific angle (steep or shallow) was of greater importance for utilization.

Further work in the area was completed during the 1970's by Bartstra (1978,1982). He discerned three terrace systems in the volcanic, clastic bedrock region of the river valley, however, the extended terrace system did not occur in the karst region of the river valley. The lowest terrace consists of two levels at 2 and 5 meters, the middle terrace is at 10 meters and the highest terrace occurs approximately 20 meters above the present riverbed. Bartstra found crude chopper tools mixed with relatively advanced Neolithic tools such as gravers and borers in the high terrace. Also, well made handaxes were found without longitudinal flaking technique, similar to West European bifaces. Thus, there is evidently a long tradition of core tool manufacture in the area, from the Early Paleolithic until the early prehistoric period. The differences between the earliest and latest specimens may only be traced in a tendency toward smaller size, in the refinement of manufacturing techniques and a change in preference for the raw material: from silicified tuff to silicified limestone. Bartstra (1978) concludes that alluvial gravels which lack fossils extend up the valley sides to 28 m. above the stream bed, but due to slumping and colluvial movement, it is not possible to correlate terrace remnants or to recognise individual terraces. In addition, origin of the terraces may not be related to glacial and interglacial periods, but rather to local uplifting during the Upper Pleistocene.

Although there is not a single site on Java where lithic tools can be clearly associated with *Homo erectus*, their artifacts must exist considering the presence of lithic tools in association with hominids in China and East Africa. It is possible that further research will ultimately provide evidence of older Quaternary deposits containing recognisable tool types (Hutterer 1977,1985).

However, Bartstra (1982) suggests it is time to stop searching for the established core types of the chopper/chopping tool complex because these may constitute a late development in Java. Instead, the research strategy must be altered to search for small, indistinct, irreglar flakes with an absence of distinct forms and types, similar to those first found by Koenigswald. The question remains if it will be possible to recognize these amorphous flakes from the naturally occuring eoliths in the area.

Yi and Clark (1983) advise that Movius' classificatory scheme shoud be discarded and appropriate morphological and technofunctional lithic typologies must be chosen. Interassemblage differences and similarites must be assessed quantitiatively. Also, geochronometric and biostratigraphic divisions which link archaeological localities must be established in order to explain interregional diversity and continuties (Hutterer 1985).

In summary, there have been many criticisms of Movius' original classification and interpretations. Presently, there are questions related to: problems of lithic typology which are based on intuitive sorting and patterned after European models; the distribution of the chopper/chopping tool tradition over regional areas; doubt about the depositional environment; controversy regarding stratigraphic correlations between sites; and lack of representative sampling. Undisputed evidence of hominid material remains could clarify the controversies by contributing to the culture-history of the area and to greater understanding of human bio-social evolution. Unfortunately, at the present time it is difficult to connect the core and flake assemblages from China and Indonesia into an integrated scheme. The reasons for this failure are that Paleolithic research has proceeded at a different rate in each region, with unequal resources, unequal capacities for observation, excavation, interpretation and publication.

Therefore, evidence for technological continuity between China and Indonesia is inconclusive; however, another variable pertinent to the problem of establishing hominid isolation and continuity in Southeast Asia during the Pleistocene may be provided by reviewing the evidence for faunal continuity. That is, if the area was geographically isolated from Western influences during the Pleistocene, this may be reflected in the absence of faunal exchanges. Following is an analysis of paleoecological and geological factors preventing or contributing to faunal and hominid migrations from China through Indonesia into Australia.

CHAPTER. 3. EVIDENCE FOR FAUNAL CONTINUITY

3.1. Paleoecology and Geology of China

North-western China is an arid region where the world's highest mountains (8,848 metres) alternate with the world's largest basins, deserts and plateaus. The Tibetan Plateau (4,500 metres above sea level) accounts for approximately one-quarter of the country's land area. The Himalayan mountain system and the Gobi Desert have been major barriers to the north and west of China for over five million years. Although this rugged area has always been highly marginal to human exploitation, the broad low-areas of Eastern China provide a contrast of extensive, fertile, alluvial plains (Renzhang 1985). The western uplands are steeply dissected horizontally on a west-east axis, thus the major rivers flow eastward into the Pacific Ocean. These large river valleys seldom run through different major climatic and vegetational zones; thereby they serve as a basis for the cultural and geographic subdivisions of China (Chang 1977).

The subdivision of China into northern and southern sections has also been a significant demarcation throughout the entire period of human occupation. Three ecological zones can be distinguished: the southern deciduous zone, the northern forests and the steppes (Chang 1977). The deciduous forest and the broadleaf evergreen forest which dominate southern China have implications for human ecology. For example, no species dominates the faunal spectrum and heterogeneity characterizes the plant and animal forms present in the ecosystem. Intra-regional variation or heterogeneity in plant and animal forms is paralleled by heterogeneity in human systems at any point in time. Thus, the differences which are exhibited among the material remains are best seen as habitat, seasonal and activity-specific differences, and not indicative of major systemic contrasts (Aigner 1978).

Initial relationships between European and Chinese fauna can be seen during the Pliocene, after the European Villafranchian faunal suite had developed throughout Western Europe, North Africa and India. By three million years ago, the Eurasian faunas had evolved from the Villafranchian, with the appearance of elephants, cattle and one-toed horses (Hooijer 1975). Aigner (1978) has argued that although the Pliocene Hipparion (or Pontian) fauna of China is related to the Eurasian Villafranchian assemblage, the North China zoological province formed an individualized assemblage with the introduction of gazelles, antelopes and many varieties of subtropical deer (Aigner 1978, Whyte 1984). Faunal exchanges with the West via a northern route were not significant in the appearance of the earliest Chinese Pleistocene species. In northern Eurasia, the Villafranchian lasted until one million years ago, when the succeeding Middle Pleistocene fauna appeared with the onset of extensive lowland glaciation. Massive extinctions of giraffes and Mastodon occurred and the northern fauna were replaced by a paleoarctic fauna; but largely through local Chinese evolution with additions from a Southeast Asian corridor. For example, the main evidence of Chinese exchange with extra-Chinese faunal provinces comes from the Stegodon assemblage, whose members may be traced to south Asia. The only exception is the introduction of *Equus*, from the north, who moved in from the New World into North China. Therefore, most of the faunal elements in both North and South China evolved in eastern Asia from Pliocene generic ancestors. At the same time, the north and south exhibit differences related to climatic-vegetation conditions and accessibility from other regions (Aigner 1978, Whyte 1984).

During the late Pleistocene, the differentiation of faunas into separate complexes was less pronounced in the forests of south China and southeast Asia than anywhere else in the world at similar latitudes (Whyte 1984). Pleistocene changes in the zonation of vegetation and fauna would have been most heavily felt in the Yangtze Basin. Other parts of southern China presented a similar heterogenous mix of habitats to human occupants in both cold and warm periods. While habitat size and location was varied, the changes within a region were quantitative rather than qualitative, in contrast to more northerly latitudes (Whyte 1984).

Luchterhand (1978, 1984) has presented a model of continuity in his analyses of climate and mammalian evolutionary patterns during the Middle Pleistocene in Eastern Asia. Conclusions apparent from the fossil record are that the structural differences which exist between the modern faunas of the northern and southern regions are of considerable antiquity, with the origins of the differences extending well back into Tertiary time. Also, the southern fauna has a long history of relative isolation from other faunal regions, while the northern faunas of East Asia show strong influence from other parts of the Paleo-Arctic. Luchterhand (1984) further states that the Middle Pleistocene hominid sites of East Asia are distributed in two widely separated areas. One group of sites is found in Southeast Asia and the other occurs in the part of North China where the deciduous forest vegetational community is grading into the arid grasslands. In the southern region, there are only three sites that have yielded actual homind fossil material, and all are in Java. Sites from the Middle Pleistocene from the northern region include only two localities i.e. Zhoukoudien and Lantian.

Middle Pleistocene hominid sites of South China are all associated with local occurrences of broken ecological systems. They are found either in areas with open grassland vegetation, on beaches, or river terraces (Whyte 1984, Luchterhand 1978). The open grassland communities are azonal features of South Asia and occur in areas where rainfall is insufficient to maintain a climax forest community. Also, beach and river terrace areas are, by their nature, regularly disrupted by short-term variation in water level, erosional activity and by the long-term variations in late Cenzoic climates and sea level (Luchterhand 1984, Whyte 1984).

The sites of North China also fall within an area of disrupted environmental conditions, but, in this case, environmental disruption is zonal rather than local in nature. The hominid sites of North China that date to the Middle Pleistocene are associated with a pan-Paleoarctic fauna that apparently evolved in direct response to the climatic fluctuations of North Eurasia during the late Cenzoic. Thus, their chronological and zoogeographical affinities suggest that they are more closely related to the Middle Pleistocene hominid sites of Western Eurasia and Northwest Africa than they are to the Middle Pleistocene counterparts in South Asia. They are separated from the South Asian sites by the undisrupted Oriental faunal region and are associated with the European occupations via a common affinity with the pan-Paleoarctic Middle Pleistocene fauna. Therefore, the hominid radiation and the broader mammalian radiation are related to vegetational communites that had been seriously disrupted by Pleistocene climatic events (Luchterhand 1978, 1984).

This data has important implications for understanding the range of local adaptive patterns, lithic assemblages, and types of sites that were present throughout Asia during the Middle Pleistocene. Rather than positing a single niche or subsistence pattern as characteristic of *Homo erectus* populations, it seems reasonable to expect regional variability in hominid adaptation. This regional variability is supported by the location of *Homo erectus* sites in north-temperate, south-temperate and tropical *Homo erectus* sites (Shutler-personal communication). It is possible that the relative maturity and degree of disruption of any given local ecological system was the most important factor in determining the success of human adaption there. This viewpoint suggests it is unlikely that a hominid entering a new and broken ecological system would do so as a carnivorous specialist. Rather, it is more likely that his primary subsistence pattern was one of broad-spectrum gathering.

Luchterhand (1984) and Whyte (1984) also re-examine conclusions concerning later hominid populations in relation to paleoecological factors. It is often suggested that Late Pleistocene archaeological assemblages show greater internal diversity and variability than do earlier ones, thereby implying an evolutionary advance. It may be necessary to consider what part of this increased diversity and variablility can be understood in terms of increasing maturity of local ecological systems, rather than only in terms of different stages of human physical or cultural development. Increased diversity and variability in archeological assemblages may reflect the general maturing process of the ecological systems in which humans found themselves during the Middle and Late Pleistocene. Only when the relations between local ecological systems and the human populations they contained are understood against the general developmental changes in Middle and Late Pleistocene ecological systems, will it be possible to generalize about how much of the change in hominid adaptations is actually due to changes in the hominids themselves. Once done, however, the results should lead to much clearer understanding of hominid adaptation, the environmental setting and evolutionary process by which man moved to his present ecological positon.

By examining the fundamentally different structures of the Chinese northern and southern faunas, Aigner (1978) and Luchterhand (1978, 1984) have stressed the hypothesis that there was minimal possibility of diffusion of Paleoarctic forms across the Oriental faunal region. Thus, they believe the data base in eastern Asia is consistent in documenting conservatism, isolation and continuity in the regional evolution of faunal assemblages.

However, Pope (1982, 1988) disagrees with the hypothesis of relative isolation and lack of migration between Chinese and Western faunal structures. He states that the uniqueness of northern Chinese faunas have been overemphasized by researchers. He argues that the movement of such mammals as camelids and giraffes along a latitudinal zone from West to East is more likely than regional movement within a specific geographic area. By the middle Pleistocene, northern Chinese faunal assemblages seem to be more comparable to western faunal assemblages from Europe and southwest Asia than to faunal assemblages from south China and southeast Asia (Pope 1982, Braches and Shutler 1984b). Also, Li (cited in Pope 1982:313) believes that in southern China distinctions between early, middle and late Pleistocene faunas are subtle and have been overemphasized. This situation may also characterize the classification of the Indonesian faunal structure (Pope 1982, 1988, De Vos 1982, Hooijer 1975) as discussed below.

Following is an examination of the geology and paleoecology of the Indonesian Islands. Ecological factors that may have affected faunal and human migration patterns throughout Indonesia are discussed for the purpose of understanding biogeographic variables influencing further southward expansion.

3.2. Paleoecology and Geology of the Indonesian Islands

Geologically, the Indonesian islands of South East Asia are volcanic peaks arising from the Sunda continental shelf. The tectonic edge platform of the Sunda shelf is under subduction with the Sahul shelf of Australia-New Guinea and has been very unstable before and during the Pleistocene.

This arc-belt consists of young, folded mountains with extensive active volcanoes and has produced many of the irregularly shaped islands found between the two continental shelves. During periods of mid-latitude glaciation, lowered sea level exposed both shelves and provided land bridges between the island areas. The history of mammalian migrations and human settlement is closely linked with the alternating submergence/emergence of these continental shelves and the complex processes of tectonic island formation (Braches and Shutler 1983,1984; Bellwood 1985).

During glacial periods, land mammals were able to migrate from mainland Southeast Asia to the islands of Sumatra, Java and Borneo across the open Sunda shelf (Fig.1) The Makassar Strait between Borneo and Sulawesi (Celebes) is sufficently wide and deep to act as an effective barrier to the dispersal of a number of mammalian species of Asiatic origin. However, the Lesser Sunda Islands chain extending east from Bali was accessible by periodic land bridges, thereby allowing Indo-Malaysian species to enter Flores and Timor. Most Australian fauna (except the genus *Phalanger*) were unable to cross the deep Timor Strait between Sahulland and Timor (Hooijer 1975). Thus, the biogeographical Wallace Line, which forms the western boundary of the Wallacean faunal zone, differentiates the placental mammal fauna of Southeast Asia from the marsupial mammals of Australia (see Fig.1)

During the 1930's Von Keonigswald's interpretations of the fossilized vertebrate land fauna resulted in a framework of faunal correlations through the Pliocene and Pleistocene. During the Pliocene, the Villafranchian fauna from Eurasia mixed with the fauna from southern India, and formed the Siva-Malayan fauna in Southeast Asia. By the beginning of the Pleistocene a new faunal suite appeared in Java, Sumatra and Kalimantan, which shared more species with southern China than did the preceding Siva-Malayan fauna (Koenigswald 1949). The new Sino-Malayan fauna developed though seven biostratigraphic units of which the last three units (Jetis, Trinil and Ngandong) have been associated with early hominids in Java. The Jetis fauna contains orangutan, gibbon, tiger, panther, water buffalo and extinct genera such as *Stegodon* and *Ailuropoda* (giant panda) which links them with contemporary faunas in south China.

Koenigswald's original faunal correlations were presented during the 1930's as a preliminary model, however, they have often been utlized as the recognized standard (Shutler and Braches 1985, 1987). Recently, Braches and Shutler's (1984a) reconsideration of the Cijulang fauna (Siva Malayan) reflect doubt that the few fossils found are sufficiently distinct to warrant its classification as a separate fauna. Also, there are questions regarding the presence of two separate faunal assemblages. They suggest that the faunal correlations for southeast Asia are out of date and require a new comparative analysis (Shutler and Braches 1985,1987).

It is now known that the collections of Jetis and Trinil fauna (which are the basis for the definition of Pleistocene faunal assemblages) contain materials lumped together from several different localities. Also, many of the fossils come from fluviatile gravel deposits which have undergone secondary transport, sorting and mixing with older deposits (Hutterer 1985). In addition, there is uncertainty regarding definite dating for the division between Jetis, Trinil and Ngandong fauna. That is, major controversy exists regarding inter-site stratigraphic correlations. Consequently, there is continuing debate over the assignment of (faunal, hominid and artifact-bearing) units from local sequences to the subdivisions of the idealized framework (Hooijer 1975, Hutterer 1985, Shutler and Braches 1987). There are also problems with tracing the geomorphological sequence of Pleistocene terraces associated with the Solo river and there is uncertainty as to the extent of stratigraphic gaps in the sedimentological record of the Pliocene and Pleistocene (Hutterer 1985). These questions concerning the biostratigraphic sequences make the dates of associations between extinct fauna and hominid remains uncertain; thereby indicating that the time period could span from 1.3 million years ago to less than 500,000 B.P.(Shutler 1983,1987).

Debates also exist about evidence for the earliest faunal migrations during the Pliocene, when two major dispersals moved eastwards. One migrated from Java along the Lesser Sundas to Flores and Timor, the other moved from Borneo to Sulawesi. They are characterized by the Cabenge fauna which includes *Stegodon*, pig, the pig-like babirusa, the buffalo-like anoa and the giant land tortoise (Bellwood 1985). The question of how the fauna moved across the area continues to be controversial (Shutler and Braches 1985). Braches and Shutler (1984b) argue that the Philippines did not play a major role in the Pleistocene dispersal of the so-called Sino-Malayan fauna to the Indonesian islands.

Hooijer (1975, 1982)) has discovered that separate large and pygmy species of *Stegodon*, derived from Java, once existed in Mindanao, Sulawesi, Flores and Timor (see Fig.1). However, Flores is now separated from Timor by the 3,000 metre deep Suva Sea, which is 150 km. wide and narrows to 30 km. between Alor and Timor. To explain these distributions, Audley-Charles, Hooijer (1973) and Hooijer (1975) suggest that Flores and Timor were joined by a land bridge during the Early Pleistocene, before the subsidence of the present Timor Sea. They argue that the Pleistocene orogenic phase in Timor resulted from a collision between the Australian continental crust and a subduction zone which lay south of the volcanic island chain of Flores, Alor and Wetar. Following the cessation of subduction, a period of island uplift occurred. They conclude that the two eastern arms of Sulawesi and the far eastern islands closest to Australia (Timor, Seram, Beru and Halmahera) were once part of the Sahul continental shelf (Audley-Charles 1973, Hooijer 1975,1982). This idea is supported by paleomagnetic results from Salawesi which suggest that the islands off the eastern arm of Sulawesi are displaced crustal fragments from New Guinea (Haile 1978).

Other researchers do not accept these postulated land bridges because of the degree of tectonic movement which they demand. Sondaar (1981) suggests that *Stegodon* moved from Sundaland into the Lesser Sundas by swimming. Thereafter, the genera underwent independent dwarfing as a result of separate selection due to isolation.

However, evidence for possible land bridges (Chappell and Thom 1977, 1982) indicate that many of the Wallacean islands are subject to specific types of tectonic instability; thus they can rise and fall independently of sea-level changes at quite rapid rates. For example, while Northern Timor is rising at the relatively slow rate of 0.5 meters per thousand years, north-east New Guinea is rising at the rapid rate of 4 metres per thousand years. Thus, there is a possibility that presently undetected islands/land bridges may have emerged during the past two million years.

The tectonic submergence and emergence of islands in Indonesia is only one factor in the history of mammalian migrations and human settlement. Another factor includes the consequences of mid-latitude glaciations. Although Island South East Asia was glaciated only in the highlands of Borneo and New Guinea, the effects of mid-latitude glaciations were strongly felt in the tropical latitudes (Bellwood 1985). Besides the well-known effects of lower sea-levels, lower temperatures (7-8 degrees Centigrade), and lower vegetation zones, an additional effect was a change in rainfall patterns. Due to an increased pressure gradient between the Asian and Australian continents, the Intertropical Front may have moved outside present limits for longer periods, leading to longer dry seasons and lower rainfall. Thus, tropical climates on large land masses became drier and existing deserts were extended over wider areas. In addition, lower temperatures reduced convectional rainfall, and winds were drier after crossing larger land areas (Bellwood 1985). This suggests that present equatorial rainforest areas may have once been relatively larger areas of monsoon forest. As a result, the longer dry seasons and more open vegetation, would have allowed easier movement of fauna and hominids southward.

These paleo-ecological changes would have greatly affected possible migrations during periods of mid-latitude glaciation when land bridges in Sunda and Sahul were connected at approximately 150,000 115,000, 90,000, 55,000, 35,000, and 18,000 B.P. Specifically, the land bridge connection at 150,000 B.P. was the period with the deepest drop in sea level, and lasted almost 20,000 years (Chappell 1983). The possiblity that *Homo sapiens* was able to take advantage of this early, extra - expanded continental shelf exposure and migrate, by island hopping in raft watercraft to Australia has been a question for continuing debate.

Birdsell (1977) has described the probable routes for Pleistocene watercraft between the Sunda and the Sahul Shelf. He discusses the three variables on the routes including: the distance to be travelled, the visibility of the island destination from the point of departure and the general size of the target island. The northern route from Sunda to Sulawesi to New Guinea involves longer water crossings up to 65 km., while the southerly passage from Java across initally small water gaps involves a terminal stretch of 87 km. It is possible that the earliest colonists used bamboo rafts to carry them eastwards by the north-west monsoon winds (Birdsell 1977). Computer generated simulations indicate that a founder population can be derived successfully from the voyagers in a single small water-craft (McArthur cited in White and O'Connell 1982). In a recent study, Shutler (1991) discusses the adaptive subsistence strategies possibly utilized by anatomically modern groups as they crossed Sundaland and colonized Sahuland (New Guinea and Australia and Tasmania).

Clearly, the paleoecological and geological evidence indicates that there was a potential route for periodic faunal and hominid migrations from southeast Asia to Australia. Ecological factors such as the presence of a water barrier, changing topography due to fluctuating sea levels and tectonic activity may have been sufficiently restrictive to prevent further southward migration. However, paleoecological factors may have assisted human migration as much as hindered it. That is, the presence of a 65 km. water barrier may have been short enough to allow accidental crossings. Also, the geological evidence of frequent, complex tectonic uplift/submergence of islands in Wallacea suggests that presently undetected islands/land bridges emerging during the past two million years must be considered a possibility. In addition, evidence for the deepest drop in sea level at periods from 150,000 - 55,000 B.P. may have shortened the water barrier sufficiently to contribute, for relatively short periods, to the migration of hominids to Australia. The question remains, however, regarding the phylogenetic affinities between southeast Asian and Australian populations. In order to understand the possible correlation between hominids in this area, it is first necessary to review fossil sites in China, Indonesia and Australia and to analyze evidence for the existence of transitional forms with regionally distinct features that continue through time.

CHAPTER 4. EVIDENCE FOR MORPHOLOGICAL CONTINUITY

4.1. CHINESE SITES:

4.1.1. Lantian

Analysis of remains at Lantian (Chenjiawo, Gongwangling, Fig. 2) indicates the mandible and cranium morphology is relatively more primitive than other fossils from Southeast Asia. For example, the Lantian specimen's supraorbital tori are massive and heavy, extending laterally much farther than the Javanese specimens. The central portions arch downward and do not meet at the middle of the face. The left temporal bone is heavily buttressed and shows a broad temporal fossa. The postorbital constriction is also more pronounced and both the frontal squama and cranial vault are very low. The cranial bones are thick and the calculated cranial capacity of only 780 cc. is smaller than that of the Javanese specimens (Wu and Dong 1985). The maxilla is broad and deep, with widely spaced incisor sockets for the anterior teeth and the base of the cheek begins in a more anterior position than the Indonesian palates. The robustness of the mandibular body, the form of the alveolar arch and the multiplicity of the mental foramen all suggest ancestral affinities to Zhoukoudien fossils (Wu and Dong 1985). Aigner (1983) supports this hypotheses and suggests that the Lantian hominids are stratigraphically older than the fossils at Zhoukoudien. Pope (1982, 1984) argues that most of the Asian hominids are less than 1.0 million years old.

4.1.2. Yuanmou

The site of Yuanmou in south central China (see Fig. 2) has yielded only the upper right and left central incisors of a single individual. Morphologically these teeth resemble those of the Zhoukoudien Locality 1 (see below) in their size, the presence of shovel-shaped surfaces, well-developed basal tubercles and finger-like projections. However, certain features of the teeth suggest some differences exist. For example, the distal portion of the crown of the Yuanmou incisors is more expanded than that of specimens from Choukoutien. Also, at Yuanmou the finger-like projections are situated on the lateral half of the lingual surface with one ridge in the middle being particularly well developed and extending almost to the cutting edge of the tooth. In the Zhoukoudien hominids, these finger-like projections are shorter and are situated in the center of the lingual surface (Wu and Dong 1985).

At the present time, the age of the Yuanmou specimen is uncertain. The teeth were originally attributed to the early Pleistocene on the basis of biostratigraphy, faunal correlation and palaeomagnetic data which suggested an early age of 1.7 million years ago (Jia 1980). However, recently accumulated bio-litho-magneto-stragigraphic data indicate the fossils are no older than the Brunhes-Matuyama boundary and may be only 500,000 to 600,000 years old (Xinzhi and Wang 1985).

4.1.3. Zhoukoudien

Originally spelled Choukoutien (see Fig. 2), this limestone cave contains one of the largest hominid collections from a single site. Fossils were deposited in this cave during a period from approx. 400,000 - 200,000 years. The deposits that include *Homo erectus* are divided into 13 layers and provide evidence of gradual changes in skeletal morphology (Wu and Lin 1983). Remains of more than forty individuals show characteristics that indicate they derive from a relatively more progressive group of individuals than do the Lantian specimens (Wu and Dong 1985). Crania recovered from layer 10, layer 9-8 boundary and layer 3 show a gradual change in cranial capacity from 915 cc. to 1,140 cc. While cranial size is larger than specimens from Lantian and Java, the Zhoukoudien crania remain long and low with the greatest breadth at the cranial base. In contrast to the Lantian fossils, they exhibit less pronounced lateral extension of the supraorbital tori and less postorbital constriction. The thickness of the cranial walls is not as great as that of the Lantian calvarium, but much thicker than that of modern *Homo sapiens*. The low vault and large nuchal torus result in an angled occiput, but in contrast to earlier specimens, there is a distinct bulge in the center of the frontal bone. This feature results in a higher forehead and accentuates the sulcus between the browridge and the forehead (Wu and Dong 1985).

Skull 5, found in Layer 3, dated approximately 230,000 B.P. exhibits morphological features that are more progressive than those of crania from deposits in Layers 8-10 dated approximately 400,000 B.P. The younger skull possesses slender supraorbital tori, a reduced occipital torus, thinner cranial walls, an arched parietal margin on the temporal bone and a foreshortening of the distance between external and internal protuberances (Wu and Lin 1983).

Two developments mark the dental samples at Zhoukoudien. First, the posterior molars are reduced in size compared to *Homo erectus* teeth from Africa and Indonesia. The second development is in the anterior dentition whereby, expansion occurs in the transverse breadth of the lateral maxillary incisor. Minimal change occurs in the central incisor, thus, the first and second incisors become more similar in size. The lingual surfaces of the upper incisors are typically shovel-shaped (Wolpoff 1980).

The mandibular samples show more variation than the cranial samples although all are characterized by large size and robustness. The entire sample is intermediate between the earlier Sangiran and later Trinil specimens from Indonesia. The symphysis is large and angled, possibly due to large anterior dental roots. The chin, however, is not yet observable. The vertical ramus is high, similar to the African and Indonesian mandibles (Wolpoff 1980).

The post-cranial remains consist of femur, humerus and tibia fragments and shafts. The limbs are similar to those of modern humans, except they are characterized by adaptations that increase the strength of the bone and its ability to withstand compressive and bending forces. Anteroposterior flattening of the shaft and thicker cortical bone of the shaft walls result in smaller medullary cavities in the post cranial skeleton (Wu and Dong 1985).

4.1.4. Hexian

The Hexian (see Fig. 2) specimens include a cranium, mandible and four isolated teeth associated with mammalian fossils dated to the Middle Pleistocene. Many details of the skull resemble those from Zhoukoudien Locality 1. For example, fossils from both sites exhibit a low cranial vault, flattened frontal bones, developed supraorbital and occipital tori, relatively thick cranial bones, a sagittal crest and similar cranial capacities. However, certain progressive features are observed in the Hexian individual. For example, the postorbital constriction is less pronounced and the temporal squama is high with an arched parietal margin similar to Skull 5 from Zhoukoudien. The distance between the external and internal protuberances of the occipital area is relatively shorter than any of the Zhoukoudien crania. These data suggest the Hexian fossils can be compared with the more advanced, later forms of *Homo erectus* at

Zhoukoudien, exemplified by Cranium 5 (Wu and Dong 1985, Xinzhi 1985).

4.1.5. Dali

A nearly complete cranium (see Fig. 2) of a male approximately thirty years old, was found in 1978 in fluvial deposits in Dali County, Shaanxi Province, north China (Wu and Wu 1985). Although the Uranium dates on associated mammalian taxa range between 200,000 - 230,000 years, there is considerable doubt regarding the age of this specimen. Morphologically the cranium has a massive supraorbital torus, a low, flat frontal, very thick cranial vault, and an angulated occipital with prominent transverse torus. The cranial capacity is 1120 cc. (slightly exceeding *Homo erectus*), although the parietals are far more expanded with less post-orbital constriction than *Homo erectus*. The mid-facial region is broad, short and flat with no midfacial prognathism. The height of the maxilla is comparable in vertical dimensions to Sangiran 17 from Java but dissimilar to Neandertals (Pope 1991). In mid-facial dimensions, Pope (1991) found the Dali specimen to be most similar to Jinniushan from northeast China.

4.1.6. Jinniushan

A cranium and partial skeleton were found in 1984 from Jinniushan Cave, Yinkou County. Tentative Uranium series dates on associated faunal remains suggest an age between 230,000 - 290,000 B.P. but the hominid may be substantially younger. This specimen has features reminiscent of *Homo erectus*, but also anticipates modern *Homo sapiens*. For example, it has a prominent supraorbital torus, although to a lesser degree than Dali. The cranial capacity is somewhat higher, estimated at 1300-1330cc. with a relatively rounded occiput. Unlike Dali it has extremely thin cranial bones, however, an occipital bun or swelling is clearly present (Pope 1991). Both Dali and Jinniushan may exemplify the same basic early *Homo sapiens* population of China.

4.2. JAVANESE SITES:

4.2.1. Sangiran and Trinil

The major sites for the Javanese fossils (Fig. 2) have been in the upper Pucangan and Kabuh deposits exposed at Sangiran and Trinil. The first *Homo erectus* cranium was found at the site of Trinil, but the majority of the early specimens come from the Sangiran site (Sangiran 2, 3, 4, 10, 12, 17). These specimens appear morphologically to be the oldest in South and East Asia, dating from 1.1 - 1.3 million years ago (Pope 1984). As previously mentioned, bio-stratigraphic data from Java are so imprecise due to secondary redepostion that no absolute date for hominid appearance is reliable at the present time (Hutterer 1985).

The Sangiran 4 speciman (previously called *Pithecanthropus* 4) comes from a stratigraphically high position in the upper Pucangan beds. The fossils consist of a robust posterior cranium and maxillae which show evidence of heavy musculature, vault thickening, spongy bone development at the cranial base, thick nuchal torus, pronounced sagittal keel and a cranial capacity of approximately 900 cubic cm. (Wolpoff 1980). The associated maxillae is also primitive with large canines projecting below the level of the adjacent teeth.

Australopithecus

Similarities are observed between Sangiran 4 and other massive mandible fragments from the upper Pucangan and lower Kabuh beds. These specimens, (previously named *Meganthropus palaeojavanicus)* are definitely hominid, but have massive teeth. Lovejoy (1981), places *Meganthropus* at the upper level of a large range of dental size variation observed in *Homo erectus*. However, Jacob (1978:20) believes *Meganthropus* should be classified as a distinct genus separate from *Homo erectus*, while Wolpoff (1980) suggests the marked size differences may correspond to a high degree of sexual dimorphism. At the present time, most researchers agree with Pope (1982), that all of the archaic Asian hominid fossils previously separated into different species can all be accomodated within the taxon *Homo erectus*.

The hominid remains associated with the younger Trinil faunal assemblage date from a wide range between 1.3 to .5 million years ago. Five fairly complete crania plus several cranial fragments represent a population less robust than the earlier Jetis fossils. The specimens fall into two size groups of large and small, which may correspond to males and females. All the specimens exhibit expanded cranial vaults, thickened cranial bone, a distinct angulation of the cranial sides at the temporal line, basal spongy bone development, thick projecting browridges separated from the forehead by a broad sulcus (groove) and expanded nuchal muscle attachments. The females (Sangiran 2, 3, 10) are smaller and thinner than the males and have weaker muscle attachment features in the temporal line, nuchal plane, sagittal keel, browridge and nuchal torus. The males (Sangiran 12, 17) are more robustly developed in the sex-related features i.e. larger mastoids and increased projection of the nuchal torus (Wolpoff 1980:191).

4.2.2. Ngandong

Located north of Trinil, on the Solo River in Java, eleven crania were recovered from a large bone-bearing deposit of extinct faunal remains (including *Stegodon*). The date of the Ngangdong fossils is questionable due to secondary dispersal among faunal bones of the gravel river bend. Also, the possible association with the extinct fauna does not provide precise dating since it is not known when key genera, such as *Stegodon* became extinct in Java (Hutterer 1985).

Santa Luca (1980) found that the Ngandong crania illustrate evolutionary changes within the *Homo erectus* range of variation. That is, he noted increased lateral expansion of the squamous temporal, reduction of the sagittal keel and a more erect plane above the occipital torus.

The trends in cranial evolution observed at Sangiran, Trinil and Ngandong, show morphological evidence of continued expansion, especially in the frontal and posterior parietal areas and in the nuchal muscle attachment area. Mandibular changes include decreased robustness and muscularity. The earlier mandibles from Sangiran and Trinil are relatively larger and thicker than the later mandibles from Ngandong, which have thinner bodies with smaller ascending rami. Similarly, dental size shows consistent change over time, with the permanent posterior teeth reducing and the anterior teeth expanding. Therefore, elements of continuity are observed from the earliest Sangiran specimens through to the more recent Ngangdong fossils (Santa Luca 1980).

While Santa Luca (1980) has classified the Ngandong specimans as late members of *Homo erectus*, Wolpoff (1980) regards them as early *Homo sapiens* due to a large cranial capacity of over 1000 cubic cm. However, Jacob (1979) and Birdsell (1977) believe the Ngandong fossils are representatives of an extinct sideline of human evolution. Thorne and Wolpoff (1981) regard Javanese *Homo erectus* as regional members of a single morphological lineage. Bellwood (1985) favours continuity tempered by periodic gene flow from Mainland South-East Asia into the peripheral region of Java. He regards the Ngandong population as a later Middle Pleistocene intermediary between *Homo erectus* of the Early Pleistocene and recent Australoid populations of Indonesia.

Therefore, the Chinese and Indonesian specimens share similar basic features in cranial morphology such as vault bone thickness, supraorbital torus development and presence of a sagittal keel and nuchal torus. However, in the Zhoukoudien crania, differences are seen in increased cranial size and the reduction of sexual dimorphism. Mandibular changes also fit a pattern of reduced robustness and muscularity. That is, the earliest specimens from Sangiran and Trinil are the largest and thickest, while the later specimens from Zhoukoudien are more reduced with thinner bodies and smaller ascending rami. Similarly, tooth size shows consistent change, with the posterior teeth reducing and the anterior teeth expanding in size. In contrast, Cranium 5, which is from a more recent level shows a higher, larger and thinner vault with a reduced browridge and an expanded occiput above the nuchal torus (Wolpoff 1980).

4.3. AUSTRALIAN SITES:

4.3.1. Kow Swamp

This population of forty adults, juveniles and children were buried in soft lacustrine and aeolian sediments on the river plain of the ancestral Murrary River system (Fig. 3). Although they have been dated 10,000 - 14,000 years old, the fossils (including children) exhibit surprisingly archaic features in the robust mandibular body, the thick vault bones of the cranium and the broad prognathic faces. Primitive features in the frontal regions include marked recession with the frontal curvature index which overlaps the range for *Homo erectus*. The males have massive browridges with thickened zygomatic bones. Five crania show a definite supraorbital torus and all crania have poorly filled temporal regions that produce a high degree of postorbital constriction. Beneath the occipital torus the nuchal plane shows well-developed muscle impressions with an external occipital crest (Thorne and Macumber 1972).

The mandibles are extremely large and cannot fit a cast of the African Rhodesian cranium. The molars are also robust with ridged tuberosities and the thick canine roots produce bulging of the buccal plate. Pronounced attrition and exposed roots of most teeth (especially the mandibular first molars) and the extensive masseter muscle fossae in the rami indicate severe masticatory stress (Thorne and Macumber 1972;, Thorne 1976,1977).

This morphology contrasts with the nearby Lake Mungo fossils, whose exremely gracile crania and mandibles, dated over 35,000 years old, are smaller than average for modern Aboriginal females. The Mungo type exhibit high, rounded more modern-appearing crania with expanded frontal and temporal regions, slight brow-ridge development, thin vault bones, short delicate faces and relatively small palates, mandibles and teeth (Bowler and Throne 1976). When comparing the Lake Mungo crania with museum collections, Thorne found there are no significant differences. The Lake Mungo crania are within the range of variation observed in eastern Australians. Thorne (1976) also compared the Kow Swamp and Mungo fossils with the results of studies using collections of coastal New South Wales and Queensland crania by Larnack and Macintosh (1966,1970). Thorne found that the overall Kow Swamp supraorbital region demonstrates a more extreme development. Forty percent of the Kow Swamp frontal bones have pseudo-torus or torus form, compared with 20.7 percent of New South Wales and 28.9 percent of Queensland specimens (Thorne 1976). However, a number of Kow Swamp crania (8,9,14) do not significantly differ from modern Victorian crania, except for greater overall size. There is also some similarity in the frontal and supra-orbital regions between Kow Swamp 14,15 and Mungo 3, while Mungo 1 resembles female crania from Kow Swamp 4 and 16. While a large dentition is a chracteristic of the robust fossils, only the largest Kow

Swamp molar breadths fall outside the modern range, with the remainder falling at the larger end of the modern Aboriginal range.

Controversy regarding Thorne's analysis includes questions about the representativeness of the Kow Swamp fossils. Perhaps the remains are part of a small, local, nontypical, inbred community. Calculations indicate they represent only 0.25% of the total population (White and O'Connell 1982:79). My response is that accepted assumptions regarding the evolution of australopithecines, Neandertals, and Erectus populations have been based on much smaller, non-represenative samples from Africa, Europe and Indonesia. In fact, the Kow Swamp population is the largest sample of pene-contemporaneous hominid fossils known at the present time. In addition, recent analysis of crania from other sites such as Talgai (Northeast Australia), Cossack (Northwest), Cohuna, Willandra Lake Hominid 50 (W.L.H.50), and Mossgeil (Southeast) also show robust characteristics. In particular, the robustness of the Cossack skull and the W.L.H. 50 are more extreme than the skulls from Kow Swamp, with very thick cranial bones, severely sloping forehead and prognathic features. As indicated on the map several of these robust skulls were found 5000 km. from Kow Swamp in the northwest of Western Australia, demonstrating that the robust population was not confined to the Kow Swamp area (Flood 1983).

Although visual inspection has shown the robustness of the Kow Swamp fossils, Thorne's comparative statistical analysis (univariate and multivariate) has come under criticism because analysis of Mungo fossils is based on measurements at the base and back of the cranium, while frontal and facial measurements are emphasized in the Kow Swamp fossils (White and O'Connell 1982).

Another explanation for the fronto-facial differences have been hypothesized by Brown (1981), who suggests the primitive features are due to artificial cranial deformation. His analysis of Melanesian and Australian crania indicate that head-binding causes flattened and elongated frontal bones, low frontal curvature, greater parietal curvature and increased cranial height. Comparison with Kow Swamp skulls indicates that the Australian skulls were broad and not constricted, possibly due to the pressing of mother's hands on infant foreheads. This would allow for a high degree of variation in the amount of deformation.

However, Thorne (1976) suggests that with the extreme recession anteriorly, there should be some corresponding reaction posteriorly in the occipital region; but he finds there is no evidence of posterior distortion. Also, the size and robustness of the Kow Swamp mandibles, palates and dentition cannot be explained by cranial deformation. Similarly, the Cohuna skull, shows evidence of a flattened forehead from artificial deformation, nevertheless, the teeth and palate are very robust and much larger than the modern

Australian average (Flood 1983).

4. 4. Regional Comparisons

The surprising robustness of the Kow Swamp fossils and their general similarity to Indonesian specimens has led recent researchers to suggest the possibility of a morphological sequence between Chinese, Indonesian and Australian Pleistocene fossils. As mentioned previously, this idea began with Weidenreich (1946) and continued with Coon (1962). Other researchers have supported the hypothesis of a unitary origin whereby all modern Aboriginals are descendants from a single migration. They explain the observed genetic and morphological variation in living Aborigines arose as a result of local internal adaptation to specific environmental pressures, mutation and drift (Abbie 1951, 1960; Macintosh 1963). Abbie suggests that "Aborigines widely dispersed through...the continent are practically uniformly homogeneous" (Abbie 1963:102) and that "all the evidence points to the fact that the Aborigines, everywhere, are one people" (Abbie 1966:42).

Macintosh also supported a unitary origin, but he was the first to note the extremes represented by the gracile Keilor and the robust Cohuna crania, stating the "mark of ancient Java" lies on the crania of the prehistoric Australians (Macintosh 1965). Larnach and Macintosh (1966,1970), using features that were diagnostic for

Aboriginal crania from coastal New South Wales and Queensland, found that the Cohuna, Talgai, Mossgiel and Keilor crania "fitted within a normal distribution of modern skulls... The archaic looking group tended towards the higher index range; the more advanced looking tended towards the lower index range" (Macintosh 1971:54). They concluded that "the subjective impression of the two separate types is not confirmed by this type of analysis" (Macintosh and Larnach 1976:115). In addition, all the Australian fossils are on "either end of a continuum of a single population" (1976:114). The Australian Aborigines are not modern hybrids but ancient hybrids. They are a homogeneous people but possessing a gene pool with a wide range of variation (Macintosh 1976).

Yamaguchi's (1967) comparative analysis of the Australians and the Ainu indicates they are not related, but that both derived from a generalized upper Paleolithic or Mesolithic common population in Asia represented by Zhoukoudien Upper Cave, Liu-Jiang skull from south China and Niah skull from Borneo. Similarly, the Tabon Cave fossils from the Philippines, show similar morphology to the Australians, "as though derived from a generalized upper Paleolithic population emergent as *Homo sapiens* but not yet clearly differentiated into races" (Macintosh 1976:124).

In contrast, other researchers have supported a theory of multiple origins, whereby two or more migrations entered

Australia at different periods. For example, Birdsell's trihybrid theory suggests three population types contributed to the modern Aboriginal phenotype. Before 25,000 B.P., an initial wave of Oceanic Negritos formed the basis of the present populations of New Guinea and Tasmania. This is followed by the rugged-appearing Murrayan migration, who occupied most of eastern and southern Australia. A third wave called the Carpentarians were the most recent (post 25,000 B.P.) occupants of the northern area (Birdsell 1967, 1977).

However, Birdsell's theory is based on measurements of a non-representative sample of modern Aboriginal populations. Also, anthropometric traits such as stature, weight, head length and nasal height are subject to strong environmental influences such as diet and climate. Also, these traits are influenced by multiple genes, which makes it difficult to use any one trait in tracing comparative evolutionary histories (White and O'Connell 1982).

Another version of the multiple origins theory is Thorne's dual hypothesis, which states that Java and China were the source of two morphologically distinct and chronologically separated migrations. He states the overall combination of extreme frontal recession, pronounced postorbital contriction, supraorbital torus and the lateral supraorbital wing points directly to the migration of a robust, archaic group from Indonesia to Australia (Kow

Swamp). The more gracile group (exemplified by Upper Cave Zhoukoudian and Liujiang) originated in southern China and migrated to Australia (Lake Mungo and Keilor). The robust and gracile populations eventually interbred to form a hybrid showing variable frequencies of robust and gracile characteristics. The result of hypbridization is seen in the modern Aboriginal morphology which exhibits a large range of variation (Thorne 1977).

In order to test the dual hypothesis and regional continuity in Indonesia and Australia, Thorne and Wolpoff (1981) reconstructed the Indonesian male *Homo erectus* specimen called Sangiran 17 and compared it to male specimens from Kow Swamp. Sangiran 17, (from the lower Kabuh formation) is dated from between 500,000-750,000 B.P., and is the first *Homo erectus* cranium to retain the facial skeleton. Kow Swamp 1 and 5 are the most complete adult male skeletons and are dated approximately 10,000 B.P. The reconstructed Sangiran 17 cranium closely resembles other Indonesian *Homo erectus* specimens, especially Trinil 2, and Sangiran 2,3,10 and 12. There is marked similarity in supraorbital projection, frontal flattening, absence of frontal bossing, low temporal squama, the presence of a sagittal torus and frontal sinus development (Thorne and Wolpoff 1981).
Further characteristics of Sangiran 17 include:
1. Marked prognathism- The gnathic index of Sangiran 17 is very high (121.9) and the gnathic index reaches its world

wide maximum for living populations in Australians (Martin and Saller cited in Thorne and Wolpoff 1981:344).

2. Another clade feature is the presence of a marked ridge paralleling the zygomaxillary suture of Sangiran 17. This feature, discussed as the eversion of the lower border of the malar bone by Larnach and Macintosh (1966,1970) is very common in modern Australians.

3. Sangiran 17 and the Kow Swamp group share other features common in modern Australian Aborigines (Larnach and Macintosh 1966,1970) i.e. the rounding of the inferolateral border of the orbit, and the lower border of the nasal aperture lacks a distinct line dividing the nasal floor from the subnasal face of the maxillae. Also, in the maxilla, continuity is shown in the marked expression of dental plane curvature, from the lateral view. This is the counterpart to the curve of Spee, a normal characteristic in the mandibles of living Australians.

Finally, the degree of reduction in the face and in the posterior dentition is characteristic in Australia, Zhoukoudian, Dali, and Sangiran 10,15 and 17. The Sangiran 17 facial heights fall within the range of the Kow Swamp males. Similarly, the dimensions of the Sangiran 17 teeth (C, P3, M1-3) fall at the mean for three Kow Swamp males.

Thorne and Wolpoff (1981) note that Sangiran 17 shows characteristics that suggest regional continuity with Australian fossils. They suggest that regional morphological continuity in Southeast Asia and Australia is observed in a group of characteristics that continue as a morphological clade. They define this concept as a "fossil sequence showing both continuity over time and differentiation from other contemporary morphological clades" (Thorne and Wolpoff 1981:342). Their use of the term describes regional continuity in an evolving polytypic species, and is not used to apply to a monophyletic lineage. However, this emphasis on morphological clade characteristics does not deny the changes in grade that separate Sangiran 17 from early Holocene Australian fossils.

Factors leading to clinal differences is explained in Thorne's (1977,1981) "center and edge hypothesis," whereby the degree of polymorphism decreases toward the border of the species. That is, the *Homo erectus* crania from Africa (the "central" area) exhibit high phenotypic variation due to high gene flow, while the Indonesian hominids, at one "edge" of the range exhibit reduced variability due to reduced gene flow. Thorne states that "in Java, reduced gene flow and effective isolation over long periods leads to a monotypic form of great temporal stability" (Thorne 1977:181). Therefore, local characteristics of earlier specimens are retained in later samples (Thorne and Wolpoff 1981).

Following their comparative analysis between Indonesian and Australian specimens, Wolpoff et. al.(1984) attempted to highlight shared resemblances between the Zhoukoudian fossils and modern Mongoloids. Adding to Weidenreich's original list of regional features for China, Wolpoff includes further traits such as: an early reduction in facial size and posterior tooth size, relatively small frontal sinuses, third molar agenesis, and a low degree of prognathism. These regional features are said to have a higher frequency of occurrence on prehistoric Chinese fossils and modern Mongoloid crania than on other populations. Also, he states the Hexian cranium "resembles the Zhoukoudian remains in many details of the forehead profile, as well as in the moderate frontal boss and the rounding of the superior orbital border (Wolpoff 1985:362).

Recently, Pope (1991) has analyzed the midfacial region of fossil Asians and found support for the Continuity Model. He sampled 173 archaic and modern specimens including Africans, Europeans, and Mongoloids and found that cheek morphology differs significantly between different geographic regions. Specifically, fossil Asians have smaller upper and lower midfaces with more horizontally-oriented zygomatics, more medially-oriented malar tubercles, a distinct incisura malaris, a more inferiorly- situated zygomaticomaxillary angle and a vertically shorter maxilla. In contrast, European fossil hominids have larger facial areas, obliquely-oriented zygomatics, vertically taller maxillae, and lack a malar tubercle and incisura malaris. Additionally, several morphological traits that were previously restricted to fossil Asians (and continue to exist in a high frequency in modern Asians), can now also be observed in modern populations worldwide. This implies that gene flow and admixture proceeded from East to West and not from West to East. Thus, the persistence of Asian traits precludes the possibility of complete genetic replacement of archaic Asian populations by a relatively recent invading group from the West.

Therefore, it appears that in China, as in Australasia, the fossils show transition from local ancestral populations to modern humans who exhibit regional features. Wolpoff et al. (1984) have suggested that racial features preceded the appearance of *Homo sapiens* morphology and were carried over from local *Homo erectus* ancestors, and at the same time, regional differences in drift, selection and access to gene flow ensured that no universal patterns of modern humans emerged. Thereby, Wolpoff et. al.(1984) advocate that there has been no hominid speciation event during the last 1.5 million years, and that theoretically *Homo erectus* should be referred to as *Homo sapiens*.

Support for this perspective may be seen in the new discovery of two almost complete fossil crania recently found in northeastern China (Li and Etler 1992). These adult specimens show a mixture of features associated both with *Homo erectus* and archaic *Homo sapiens*. For example, the face is relatively flattened, the canine fossa is distinct, and there is a pronounced malar incisure. In addition the specimens exhibit a long, low angulated cranial vault, a hyper-robust tympanic region, a low placement of greatest cranial breadth, and cranial sides that slope inwards. Although these latter features characterize the taxon *Homo erectus*, typical traits that have been previously used to differentiate Asian *Homo erectus* from African *Homo erectus* are missing from these crania. The authors propose that "the differential temporal appearance of modern morphologies in regionally disparate hominids attests to the mosaic nature of human evolution" (Li and Etler 1992:407). They suggest that fossil hominid variability, as shown by these crania, indicate that *Homo erectus* traits are polymorphic within Middle Pleistocene hominids, and thereby, cannot be used to define *Homo erectus* as a distinct hominid species.

CHAPTER 5. PROBLEMS IN THE CONTINUTIY MODEL

While the case for continuity is persuasive, there are several arguments against the underlying assumptions used by this model. Stringer (1989) states that Wolpoff's comparison of Sangiran 17 to Australian fossils is not a good sample on which to base an argument for regional continuity, because it is based on a single individual, thereby giving a frequency of 100 percent for the features in Indonesia. Detailed arguments against the Continuity Model are noted in Habgood's (1986) multivariate analysis, whereby he evaluates the single and multiple migration hypotheses. He states that if Thorne is correct and the gracile Australian fossils are the result of a migration from China, (as documented by Zhoukoudian Upper Cave and Liujiang) then they should be more similar to this material than to the robust Australian fossils. In his dendrogram, Habgood (1986) notes three major clusters are evident: Australian/Southeast Asian, European/African and European. Eight smaller groupings, reflecting geographic distributions, are discernible within the three major clusters: 3 groups of Asian crania, 3 groups of European crania, 1 group of African crania, and 1 group of robust/gracile crania. The gracile crania are more similar to the robust crania than they are to crania from China (Upper Cave, Liujiang), the area from which Thorne believes they were derived. These results appear to discount Thorne's separation of the Australian crania into two morphological groups. Thus, the dual source hypothesis for the origin of the Australian Aborigines would appear to be negated. Habgood (1986) concludes that the Kow Swamp and Mungo fossils come from a single, but morphologicallly variable population derived from a single homeland. Thorne's statement that large mandibles, palates and dentition typify the robust group is explained, by Habgood, as extremes of a morphological continuum. Although Habgood's data may refute the dual origin hyothesis, it does not necessarily negate the Continuity Model as a whole. His dendrogram indicates that the robust and gracile crania together are most similar to Wajak 1 and Zhoukoudian Upper Cave 101. This suggests a similarity in grade and clade, which may reflect regional Australasian continuity.

Brown's recent results from comparative craniometric, tooth size and vault thickness studies from Pleistocene and early Holocene Australian specimens, also indicate the existence of a single, homogenous, aboriginal Pleistocene population. He believes variation within the Pleistocene group is present at an individual level (Brown 1987:61). Stringer (1992) agrees that only one anatomically modern founder population from southeast Asia to Australia was followed by rapid development of local variation. I disagree with this viewpoint, because a founder group carrying such a marked degree of dichotomous variation should be reflected in the original population from which the founder group emerged;

in fact, this so-called marked variability has NOT been observed in Late Pleistocene southeast Asian populations.

Researchers have also questioned the validity of the regional features previously mentioned by Weidenreich and Wolpoff (Habgood 1987,1989; Groves 1989; Stringer 1989). These authors state that most of the regional features are not unique clade characteristics for East Asia because they are observed as primitive retentions commonly found on *Homo erectus* or archaic *Homo sapiens* crania from other geographical areas. Also. they find that some of the features have a variable frequency in modern Mongoloid populations from high to relatively low. Therefore, these proposed regional features cannot be used to document regional continuity (Habgood 1987;Groves 1989).

However, Habgood (1989) does recognize that there is a group of features, which, in combination, may document existence of a morphological clade in Australasia. For example, a cranium that has a long and sagittally flat frontal bone with a posteriorly placed minimum frontal breadth; a very prognathic face; malars with everted lower borders; and prominent zygomaxillary tuberosities could be regarded as having a unique Australian morphology. All these features are commonly found in combination on both prehistoric and modern Australian crania, and on Sangiran 17 from Indonesia, but are not found in combination on fossils from other geographical areas. The Willandra Lakes Hominid 50 also displays a combination of the four possible regional features. However, Lake Mungo 1 and 3 (although fragmentary) do not display any of these features. Thus, there appears to be evidence in Australia, for both regional continuity and discontinuity (Habgood 1989).

Habgood has also examined skeletal material from China to ascertain evidence for morphological continuity or discontinuity. Chinese regional features that have been proposed throughout the years by Weidenreich (1943), Aigner (1976,1978), Coon (1962), Wu Xinzhi and Wu Maolin (1985), Wolpoff et al.(1984), Thorne and Wolpoff (1981), Wolpoff (1980,1985,1989), Pope (1991) were analyzed by Habgood (1992). All of the proposed traits, including for example, agenesis of the third molar, persistence of foramen of Huschke (fissure in the tympanic plate), sagittal crest, non-projecting nasal bones, flat upper faces, shovel-shaped incisors, angular zygomatic bone (incisura malaris) etc. were found to occur with various frequencies in other populations. However, a specific combination of features related to facial flatness appear to have only a limited distribution outside of east Asia. This combination of features include:

1. non-depressed nasion,
2. more perpendicularly oriented nasal bones,
3. frontonasal and frontomaxillary sutures on almost the same level, and
4. an angular rather than a rounded junction of the

zygomatic bone and the zygomatic process of the maxilla.

Therefore, as in Australasia, a combination of morphological features uncommon outside the region suggest there is a case for a certain degree of regional continuity in China.

One problem is that some late Pleistocene-early Holocene crania from China do not display all of these features. The three Zhoukoudian Upper Cave crania, dated between 18,000 - 10,000 B.P. are often seen as a discontinuity in any evolutionary sequence in China. Weidenreich noticed that each of the three crania were surprisingly different and stated they may typify different racial elements such as Mongoloid, Melanesoid and Eskimoid types. Discriminant function analysis of Upper Cave 101 have placed it near Plains Indians and suggest that the Upper Cave individuals were pre-Chinese, 'unspecialized' Mongoloids resembling American Indians (Howells 1983:301).

Therefore, in China, Indonesia and Australia, the hominid evolutionary sequence displays evidence for both morphological continuty and discontinuty. At present it remains difficult to determine whether the Regional Continuity Model best describes the origin of modern humans in Southeast Asia and Australia. As described in chapters 2-5, there are several difficulties in establishing the details of Late Pleistocene hominid evolution in the region, and the details of the peopling of Australia.

First, although the Chinese technological record suggests the possiblity of continuity, the absence of a clearly associated lithic record in Indonesia makes it difficult to allow correlations between the regions. In the past, many researchers have suggested that North and South Chinese Pleistocene technocomplexes generally show affinities to the Javanese Pacitanean industry. The classification, by Movius, of the Pacitanean chopper/chopping tool complex was used for many years as a theoretical basis to formulate assumptions regarding the technology of *Homo erectus* in Southeast Asia. However, at the present time, controversy exists regarding the stratigraphic correlation, lithic classification and typological association of this assemblage. Researchers now conclude there is no clear evidence that Pacitanean tools can be attributed to Early/Middle Pleistocene hominids.

Second, von Koenigswald's faunal correlations for Indonesia were presented during the 1930's as a preliminary model, and have often been utilized as the recognized standard. Presently, however, there is doubt regarding the presence of two separate faunal assemblages. Although paleoecological factors allow for faunal/hominid migrations at specified times, the faunal correlations for Southeast Asia may be out of date and require a new comparative analysis in order to determine the degree of isolation and continuity.

Finally, although the phylogenetic affinities within the region indicate evidence for continuity, there is also continuing debate on the relevance of regional morphological traits to determine hominid evolutionary sequences.

Researchers who, in the past, have opposed the Continuity Model now acknowledge that several factors exist favoring the possiblity of continuity. For example, Stringer (1989) agrees that the Willandra Lake Hominid 50, which is fully sapient, appears similar to African specimens which lie outside the borderline of the modern human range. This fossil may support the model of independent local evolution from an archaic Ngandong-like ancestor to *Homo sapiens* (Stringer 1989:76).

In addition, Smith et. al. (1989) state that "it is difficult to deny the existence of a sequence with strong phenetic indications of continuity between *Homo erectus* and archaic *H. sapiens* in China.... (and) assuming Habgood's analyses are correct, is seems IMPROBABLE (emphasis mine) that the appearance of modern humans in East Asia resulted from a complete replacement" (Smith et.al. 1989:52).

Thus, at this time, the Continuity Model continues to offer the most plausible explanation for the evolution and distribution of *Homo sapiens* in Southeast Asia and Australia. However, a conclusive explanation must await analysis of the Replacement Model in order to determine the merits of each side of the controversy. Therefore, Part Two of this thesis focuses on the evidence used by the Replacement Model to argue for the relatively recent origin of modern humans.

PART TWO. THE REPLACEMENT MODEL

CHAPTER 6. HISTORICAL BACKGROUND

The Replacement Model has its roots in earlier models developed after the turn of the century (Spencer 1984). Early researchers believed modern humans originated independently in Europe or the Middle East with no ancestral ties to archaic species who eventually became extinct. For example, in the 1920's Boule developed the Presapiens hypthesis, which posited the existence of a European lineage leading to modern people, but separate from the Neandertal lineage. During the 1950's, Howell presented a Preneandertal model which suggested that modern humans evolved outside Europe and were not lineal descendants of Neandertals.

There has long been a historical pattern of discomfort with the idea that Neanderthals or similar southwest Asian forms could be ancestral to early modern humans (Spencer 1984). The various versions of replacement models during the past seventy years have attempted to delegate such hominids to a path of extiniction. It is only recently that dramatic genetic evidence has provided a new twist to the question of human origins and in the process initiated a media extravaganza that has focused on the polarity of dissenting personalities rather than the dry data of science.

In the early 1970's, Chris Stringer from the British Museum suggested that South Africa and not Europe nor the

Middle East, was the central origin for the emergence of modern humans. Based on early anatomically modern fossil sites in South Africa, Stringer claimed that modern humans appeared in Africa earlier than other areas. A decade later, genetic studies on human mitochondrial DNA were published that appeared to support Stringer's idea of an African origin.

The specific use of human mitochondrial DNA (mtDNA) to track human evolution was pioneered by Wesley Brown (1979, 1980) from University of California at Berkeley. Brown determined that the minimal amount of diversity between the mtDNA of various racial groups indicated a relatively recent origin for modern humans. His analyses of mtDNA from human placentas concluded that mtDNA is especially valuable for studies of genetic variability within and among populations and among closely related species.

During the 1980's, Rebecca Cann from the University at Berkely studied the DNA from the mitochondria of cells and concluded that the mutations occurring in mtDNA are probably neutral in their effect on the body, and the changes that occur are only a factor of time; i.e. the more time has passed the greater the number of mutations will have occurred. She hypothesized that within different geographic groups, the ones with the most number of mutations in their mtDNA would be the oldest. Basing her studies on these premises, she found that Africans have the greatest number of mutational changes in their mtDNA and, furthermore, using an estimated mutation rate of 2-4% change per million years, she suggested that the oldest modern groups are approx. 200,000 years old. She also stated that these first populations with modern mtDNA gradually migrated out of Africa and replaced all previously existing populations in the Old World with no interbreeding, implying that the origin of modern humans was a biological speciation event.

This hypothesis initiated a flurry of media attention and became enmeshed in counter arguments that involved geneticists and paleoanthropologists on opposing sides. In the following chapters I analyze and critique first the chronometric and then the genetic evidence that has been used by researchers supporting the Replacement Model.

CHAPTER 7. CHRONOMETRIC EVIDENCE FOR THE EARLIEST ANATOMICALLY MODERN HUMANS

7.1 South Africa

During the 1970's, most researchers accepted the viewpoint that Africa had been a technological backwater during the Middle and Late Paleolithic. This viewpoint was supported by the chronometric evidence for a relatively late onset of Middle Paleolithic (Middle Stone Age) technology approx. 40,000 B.P., and by the persistence of an archaic physical type in South Africa long after the emergence of modern humans in Europe. New dating evidence now suggests that the Middle Stone Age (MSA) began over 100 ky ago (Deacon 1989), and that hominid remains possibly associated with the MSA indicate anatomically modern humans existed in South Africa sometime between 40,000 - 100,000 B.P. (see Brauer and Rightmire in Smith and Spencer 1984). Furthermore, several researchers argue that transitional specimens from archaic to modern humans can be documented in S. Africa. For example, archaic-reminiscent specimens from Florisbad, Laetoli, Eliye Springs, Ngaloba, Omo Kibish 2 and Jebel Irhoud are suggestive of a transition from late archaic *Homo sapiens* to modern humans that took place in Africa between 100,000 - 200,000 years ago (Brauer 1989, 1992; Smith 1992; Stringer 1989).

Evidence for early modern specimens at MSA sites have been found at three main sites in South Africa: Klases River

Main Site (KRMS), Border Cave and Omo 1. There is little doubt that all of these sites contain human skeletal remains that are essentially modern (contra Wolpoff 1989), therefore, a morphological description and comparison of these fossils is unnecessary for the purposes of this thesis.

Specifically, however, it is the accuracy of the context and the precision of the dating evidence that appears suspect. Surprisingly, this question has been given only recent, minimal discussion in the literature (Frayer 1992, Smith 1992 and Wolpoff 1989, 1992) considering the impact this controversy has to the validity of the Replacement Model. Therefore, a critical assessment of the context and dating of these three important early modern sites in S. Africa is essential to the argument.

7.1.1. Klasis River Main Site (KRMS)

This complex of overhangs and caverns along the South African coast (Fig. 4) was initially excavated by Singer and Wymer (1982). KRMS is stratigraphically divided into three major units: LBS, SAS and Upper Members. The base of the archaeological deposits, the LBS, is a series of sands with discrete intercalations of shell middens and hearths containing artifacts and fauna. LBS contains the MSA 1 technological substage and appears to date over 100,000 years. This estimate is based on oxygen isotope correlation (Wymer and Singer 1982), amino acid dating, electron spin resonance and uranium disequilibrium dating (Deacon 1989, 1992).

The deposits immediately overlying the LBS member are also sands with shell, and have been dated to approx. 90,000 years. This layer contains the main human sample consisting of very fragmentary cranial, dental and mandibular remains. Both robust and gracile individuals are represented and have been interpreted as sexually dimorphic specimens within a single population (Deacon 1989,1992). The Upper Members consist of sands 1 meter thick containing a few carbonized zones representing very episodic human occupation. During the current excavations, dental fragments and two parietal fragments were found, but they are too old to be dated by the conventional C14 method. Instead, amino acid dating and oxygen isotope correlation have been used to argue that the base of the Upper Member is greater than 60,000 years. Deacon (1989,1992), thereby, suggests an age of 80,000 - 100,000 for the SAS Member hominids.

However, several problems are apparent regarding the reliablity of specific chronometric techniques. Dating methods such as uranium disequilibrium, thermoluminescence and electron spin resonance are still at an experimental stage of development. Presently, they produce large error bars and are not routine in application. Also, the use of amino acid racemization analysis is an imprecise chronometric technique that is highly error-prone (Taylor et al. 1985).

In particular, racemization dating is based on the fact that amino acids within collagen lean refractively from left to right very gradually over geologic time; thus,the ratio of right/left refraction increases with the age of the sample (Bada 1975). However, the major factor that affects the extent of racemization in a sample is the average temperature to which the bone has been exposed, i.e. the warmer the temperature, the faster the racemization rate. Other environmental factors, such as humidity, also have effects on racemization rates. In elevated temperature studies, bones which are heated in the absence of water show little, if any, racemization (Bada 1975). Therefore, this type of analysis may be very imprecise for archaeological sites where changes in humidity/temperature throughout the past 100,000 years can not be evaluated.

Another type of chronometric technique used to date the South African sites is uranium disequilibrium analyses. Besides its status as an experimental technique, it cannot in this case, provide precise age estimates for LBS or SAS layers because uranium enrichment CONTAMINATION exists in the zone of ground water percolation (Smith 1989). Thereby, the accuracy of this date is completely skewed and unreliable!!

Problems with date estimation for the Omo and Border Cave hominids, are even greater!!

7.1.2. Omo Kibish

The site for Omo 1 (Fig. 4) was found partially in situ in Member 1 of the Omo Kibish formation (Day and Stringer 1982). The specimen was associated with faunal remains including a primitive modern elephant (*Loxodonta africana*), an advanced archaic elephant (*Elephas recki*) and both white and black rhinoceros. However, this faunal association is unconvincing of any remote antiquity (Howell cited in Smith et al. 1989:45). On the basis of uranium/throrium dating on mollusc shell, Member 1 is approximately 130,000 years old. Member 3, which lies SIXTY METRES above Omo 1 has been dated <37,000 years by carbon dating of mollusc shell.

However, mollusc shell is well known to be highly unreliable for use in radiocarbon dating. The uranium/thorium date is also equivocal, since dates on mollusc shell have been shown to have less than .5 probability of accuracy (Habgood cited in Smith et al. 1989:46). Butzer (cited in Smith 1989:45) believes that Members 1,2, and 3 all lie within oxygen isotope stage 4 and are all older than 75,000 B.P. Brauer (1989) thereby uses this evidence and suggests that an age of 100,000 years is well established for Omo 1. I disagree with this highly speculative interpretation and over-zealous use of imprecise data. Besides the use of problematic mollusc dates, it is highly inaccurate to estimate passage of time over SIXTY METRES of geological deposit in one level.

7.1.3. Border Cave

From the site of Border Cave (Fig. 4), four fully modern Border Cave specimens (BC-1 crania, BC-2 mandible, BC-3 infant skeleton, BC-5 mandible) are claimed to be older than 100,000 years. However, only 2 specimens (BC-5 mandible and BC-3 infant skeleton) were found *in situ* and associated with MSA levels dated by C-14 at >49,000. It has been suggested that correlations to oxygen isotope stages suggest these hominids date between 90,000 - 115,000 B.P.

Parkington (1990:45), however, notes that correlations between an inland site like Border Cave and isotope changes in seawater involve questionable assumptions. Furthermore, Klein (1989) suggests the hominids may be intrusive because a strong contrast can be observed in the state of preservation between the human bones and animal bones that occur in the same levels. Unlike the animal bones, which are poorly preserved and highly fragmented as a result of substantial postdepositional leaching and profile compaction, the human bones are relatively well-preserved and complete. Both Klein (1989) and Parkington (1990) state that the relatively intact condition of the Border Cave specimens suggest that the adult cranial and mandibular material have been mixed deeper into the MSA deposits and may, in fact, only date to 40,000 B.P..

Therefore, it is not presently possible to determine a precise date for any of these specimens and thus for the appearance of modern humans in Africa. The KRMS, Border Cave and Omo hominids lie outside the range of conventional radiocarbon dating, meaning they are minimally 40-50,000 years old, if one is willing to accept radiocarbon dates on mollusc shell. Also, the acceptance of ages based on thickness of deposits between levels is too imprecise on which to base wide-ranging assumptions regarding the origin of modern humans. Stringer (1992:10) concedes that "each part of the morphological, archaeological, stratigraphic or chronological evidence from these African sites is subject to some degree of uncertainty, and it is right that the evidence should be scrutinised carefully." In fact, the only conclusive evidence that can be demonstrated regarding modern humans in South Africa is that they appeared sometime after 40,000 B.P.

Based on the above arguments, it would seem there is no precise chronometric evidence dating the earliest moderns from South Africa. Another factor that may reflect complete replacement is the absence of transitional forms in Europe. While morphological evidence for transitional forms does exist in southeast Asia, as discussed in previous chapters, the evidence for transitional specimens is more complex in parts of central and Eastern Europe and Western Asia.

7.2. Eurasia

New dating information from the sites of Qafzeh and Skhul in Israel has led researchers to suggest that modern humans may have originated in Eastern Europe. A series of thermoluminescence (TL) and ESR dates lend suppport to the hypothesis that a morphologically variable population of modern humans with archaic-reminiscent features existed in this region between 80-115,000 years ago (Bar-Yosef 1992, Valladas et al. 1988)). These archaic traits include large brow ridges, alveolar prognathism, retromolar spaces and large tooth size; traits that appear to be similar to Eurasian archaic hominids.

Proponents of the Replacement Model suggest that the Skhul/Qafzeh hominids are the result of a northern migration of the initial Homo sapiens stock from south Africa (Brauer 1989, Stringer and Andrews 1988). However, regionally distinct traits such as the supra-iniac fossa (autapomorphic for Neandertals) and the pattern of alveolar prognathism in some of the Skhul/Qafzeh sample may reflect regional similarity to archaic Eurasian hominids rather than to an African influence.

Further evidence of continuity in this area is found in central Europe, where a series of late Neandertals from Krapina, Vindija Cave, Kulna Cave and Sipka Cave exhibit a pattern of facial reduction including reduced brow ridges, presence of canine fossae, vertical mandibular symphyeses, narrower anterior teeth, and narrower nasal aperatures. Some of these Neandertal specimens show only weak torus expression, higher foreheads, vault thinning and the absence of occipital bunning. (Smith 1984,1992.

Furthermore, the earliest modern specimens from central Europe exhibit a number of traits that reflect a degree of Neandertal ancestry. Post-Neandertal populations including males 5 and 6 from Mladec Cave retain seemingly unique Neandertal features such as the shape of the lateral cranial contour, supraorbital projection, lambdoidal flattening, occipital bunning, and Neandertal-sized canines. Frayer (1992) details additional autapomorphic Neandertal features (such as the H-O mandibular fossa) which extend into the post-Neandertal European populations. In addition, the pattern of brow ridge reduction (progressive mid-orbital diminution unlike the African clade), indicates a potential reflection of European continuity (Smith et al. 1989; Frayer 1992).

Finally, the attempt to associate hominid morphology with specific technological adaptative complexity in Eurasia is also problematical. The technological association of Neandertal with Mousterian assemblages and modern humans with Upper Paleolithic tools has been negated at several European sites. For example, Neandertals are apparently associated with an Upper Paleolithic (Chatelperronian) Industry in western Europe at St. Cesaire and A'rcy sur Cur. Neandertals may also have been responsible for comparable industries elsewhere in Europe, such as the Upper Paleolithic Szeletian in north-central Europe and Uluzzian industry in Italy

(Wolpoff 1992). At the same time, there is evidence that modern humans from Skhul and Qafzeh utilized a Middle Paleolithic Mousterian technology. Thus, the lack of any direct correlation between hominids and industries implies there is no technological evidence for replacement of relatively earlier populations by a new people with cultural and technological superiority.

CHAPTER 8 GENETIC EVIDENCE FOR REPLACEMENT

Prior to discussing the genetic evidence for replacement I will provide, for the benefit of non-biologists, a short introduction to the genetic terminology used in the following section. Then, a general synthesis of molecular biology of nuclear DNA and mtDNA will be discussed in order to provide relevant background for an appropriate analysis of the genetic data.

8.1. MOLECULAR BIOLOGY OF DNA - terminology

Nucleic Acids (DNA, RNA)

Nucleic acids are one of the four major classes of complex organic compounds (the other three are carbohydrates, lipids, and proteins). They are the materials of which genes, the units of heredity, are composed. They are also the messenger substances that convey information from the genes in the nucleus to the rest of the cell, information that determines the structural attributes of the cell and its functional activities. Nucleic acid molecules consist of building blocks called nucleotides, that are composed of still smaller parts: a five-carbon sugar, a phosphate group, and an organic nitrogen-containing base. The sugar used by one type of nucleic acid is ribose (ribonucleic acid or RNA), while another type of nucleic acid uses the sugar deoxyribose

Deoxyribonucleic Acid (DNA)

DNA is a type of nucleic acid with four different kinds of nucleotide building blocks. All four have deoxyribose as their sugar component, however they differ in their nitrogen-containing bases. Two of these bases, adenine (A) and quanine (G), are double-ring structures known as purines, while the other two bases, cytosine (C) and thymine (T) are single-ring structures known as pyrimidines (Watson et al.1987). The nucleotides bind together in a long chain of alternating sugar and phosphate groups that is chemically attracted to another similar chain of nucleotides that are oriented in opposite directions. These two chains, arranged side by side, are connected by their nitrogenous bases (A,G,C, and T). However, G can only bond with C and T can only bond with A to form base-pairs. The biological significance of this arrangement is that the base sequence of one chain uniquely specifies the base sequence of the other, so the two strands can be separated and exact copies made each time a cell divides. The sequence of the nucleotides in DNA encodes hereditary information or genes which are segments of DNA that code for a specific protein. In other words, the sequence of nucleotides in DNA determines the sequencing of amino acids that produce different types of proteins. The sequence in which the four different nucleotides occur is generally constant in DNA of the same species, but differs between species (Watson et al. 1987).

Ribonucleic Acid (RNA)

A second type of nucleic acid is Ribonucleic Acid (RNA). It differs from DNA in three main ways:

1) The sugar in RNA is ribose, whereas in DNA it is deoxyribose.

2) RNA does not contain thymine (T), one of the four nitrogenous bases of DNA, instead, RNA contains a very similar base, uracil.

3) RNA is single-stranded, whereas DNA is usually double-stranded.

There are three major types of RNA, each with a different role in protein synthesis. One type acts as a messenger (mRNA) carrying instructions from the DNA in the nucleus to the sites of protein synthesis in the cell. A second type of RNA exists outside the nucleus as ribosomes (rRNA), on which the process of protein synthesis takes place. A third type (tRNA) transports amino acids to the ribosomes, for incorporation into proteins.

Cell Nucleus

Organisms, such as bacteria, whose cells lack a membrane-bounded nucleus are designated as "prokaryotic" (having a primitive nucleus). All other organisms have cells which contain a nucleus that is separated from the rest of the cell's cytoplasm by a membrane designated as "eucaryotic" (having a true nucleus). The eucaryotic nucleus contains chromosomes that are elongate, threadlike bodies clearly visible only when the cell is undergoing division.

The chromosomes are composed of DNA and proteins. The DNA carries the hereditary information which is written in the sequence of the nucleotide building blocks. The protein provides spool-like supports (nucleosomes) on which the DNA is wound. While the DNA remains in the nucleus, the first phase for conveying the information from the nucleus to the outside cyoplasm is called transcription. This is a process by which the double stranded DNA unwinds and allows a copy to be made in the form of a corresponding nucleotide sequence in RNA.

A second phase, called translation, occurs when this RNA sequence and the resulting messenger RNA (mRNA) leaves the nucleus and moves to the sites of protein synthesis in the cytoplasm. There, another type of ribonucleic acid called transfer RNA (tRNA) reads groups of 3 nucleotides or codons (eg. A,G,T) which together code for a particular amino acid. The amino acids are linked into polypeptide chains to form proteins necessary for cellular functions. During these various processes of translation, transcription or replication, random changes may occur to the DNA structure resulting in mutations.

Mutations

Mutations, or changes in the sequence of bases in the DNA, can change the information content of genes. Two types of mutation are *additions* and *deletions* of single bases. That is, the insertion or deletion of nucleotides along the DNA sequence can alter the code and cause the production of another type of amino acid. A third type of mutation is *base substitution* (also called *point mutation*) in which one nucleotide is replaced by another. A nucleotide substitution does not always lead to an amino acid change because many codons may code for the same amino acid. Another type of mutation is called *transposition* which results from the insertion of long stretches of DNA from one part of the genome into the middle of another.

8.2. MOLECULAR BIOLOGY OF MITOCHONDRIAL DNA

Mitochondria are oval-shaped organelles located outside the nucleus of every plant and animal cell. They are self-replicating bodies containing genetic material that allows protein synthesis on ribosomes of their own making. They lack nuclear membranes and have a single, circular chromosome, unlike nuclear chromosomes which are elongate, threadlike bodies wound on spool-like supports, or cores. Mitochondria, the powerhouses of the cell, are the sites of chemical reactions that extract energy from food and make it available to the cell for all its energy-requiring activities. Each mitochondrion is bounded by a double membrane; the outer is smooth in appearance but contains numerous gates and pumps, while the inner membrane has convoluted inwardly-directed folds that are relatively impermeable. Fatty acids and pyruvic acid (an energy-rich product of glucose that is suitable for metabolism) are concentrated in the mitochondria. Here with the assistance of appropriate enzymes, these fuels (reactants) can combine with oxygen to produce water, carbon dioxide and energy for cell functions.

Each mitochondria contains several copies of its circular DNA, which is more similar to a procaryotic cell (non-nucleated) DNA than to the nuclear DNA of eucaryotic cells (containing a true nucleus). It lacks the histone (protein) nucleosome cores characteristic of nuclear DNA and is attached to the inner membrane of the mitochondria in a similar manner as the procaryotic chromosome is attached to the cell membrane. However, it has fewer base pairs than bacterial DNA. For example, the *E. coli* bacterial chromosome encodes about 3000 protein products, whereas, a typical animal mitochondrial genome encodes approximately 40 products, which are insufficient to carry out mitochondrial synthesis and operations.

During the process of evolution most of the genes necessary for organelle function have developed within the cell's nucleus. Therefore, although mitochondria divide, grow, differentiate, and contain their own DNA, they are not fully autonomous entities, but are controlled by the nuclear DNA. The other several hundred proteins necessary for the metabolic functions of mitochondria and all of the hundred or more proteins necessary for replication, transcription and translation and electron transport etc. must be encoded by nuclear genes and transported to the mitochondria.

The complete nucleotide sequence of the mtDNA genome from one individual has recently been determined (Anderson et.al. 1981) and has provided a great deal of the information about the molecular biology of this molecule. The mtDNAs of all multicellular animals apparently have the same set of 37 genes which specify 22 tRNAs, 13 mRNAs, and 2 rRNAs (De La Cruz et.al. as cited in Wilson 1985:379). These genes are packed within approx. 15 kilobases (16,569 nucleotides) of double-stranded DNA. The proteins specified by the 37 genes are all involved in electron transport and cellular respiration.

The mtDNA genome is unusual in its extreme paucity of non-coding features. Only about 7 percent of the mitochondrial genome does not directly code for proteins, rRNAs or tRNAs. In contrast, more than 95 percent of the nuclear DNA is non-coding. The mtDNA coding regions lack intervening sequences (introns) and intergenic regions are seldom more than 10 base-pairs in length.

Unlike nuclear DNA, the DNA sequence of mitochondria are well-known because there is less genetic information in mtDNA: i.e. 16,569 base-pairs or nucleotides compared to 400 billion base pairs in the nuclear DNA of modern humans. Also, mitochondria are abundant: approx. 9000 copies occur in one cell. There are, also, four important attributes of mtDNA that have allowed it to become the best known portion of eukaryotic DNA:

1. unisexual (maternal) mode of inheritance,
2. relatively rapid rate of evolution,
3. ease of methodological purification,
4. substantial sequence variation among individuals,

Each of these four attributes are discussed in the following sections:

8.2.1. Maternal Inheritance of mtDNA

The original discovery that mitochondria have their own genes occurred in 1938, when T.M. Sonneborn discovered that some strains of *Paramecium aurelia* carry a cytoplasmic gene which produces a poison that kills other strains. It was subsequently realized that the poison is produced by a mitochondrial gene which replicates itself. It is now known that the replication and division of mitochondrial DNA occurs out of phase with chromosome replication in the nucleus.

In animals, mitochondrial recombination of male and female gametes does not occur because the maternal gamete (egg) contributes essentially all the cytoplasm, and hence all the mitochonria (Keeton and Gould 1986:439, Stoneking and Wilson 1989:218).

Cells of the ovum are unusually large and contain a high level of cytoplasm compared to the relatively small sperm cells which contain very little cytoplasm. The ovum thus furnishes most of the initial cytoplasm for the embryo since the oocyte contains approximately one million mtDNA molecules, compared to about 50 in the midpiece of the sperm (Stoneking and Wilson 1989). Although the base of a sperm flagellum is packed with mitochondria, essentially none of these mitochondria enter the ovum during fertilization because they remain behind in the tail of the flagellum after the sperm nucleus enters the ovum.

However, researchers (Giles et al. cited in Stoneking and Wilson 1989) have found that a paternal contribution of less than 3.6 percent per generation cannot be ruled out. Studies on the question of paternal inheritance of animal mtDNA involving female hybrids were backcrossed over many generations to the parental male species, allowing any paternal mtDNA to accumulate, thereby enhancing the probability of detecting a paternal contribution. These studies were able to rule out a paternal contribution greater than 0.001 percent per generation. They concluded that while the possiblity of rare exceptions cannot be excluded, sperm contribute minimal mtDNA to succeeding generations.

8.2.2. Rapid Evolution of mtDNA

Enzymes that repair replication errors and DNA damage are not found in the mitochondria. Furthermore, the mtDNA mutational spectrum is characterized by an elevated ratio of purine-purine or pyrimidine-pyrimidine substitutions to purine-pyrimidine substitutions, and by a high incidence of small length mutations. Deleting the repair system from bacteria results in an almost identical mutational spectrum.

Wilson et al. (1985:380) suggest that the most relevant explanation for the rapidity of mtDNA evolution is the mitochondrion's apparent inefficiency (relative to the nucleus) in repairing replication errors. Thus, the effective mutation rate and corresponding evolutionary rate is higher for mtDNA than for nuclear DNA.

Spuhler (1988) states that the mutation rate is higher in mtDNA due to the more rapid somatic turnover rate of mtDNA compared to nuclear DNA. It takes approx. 1 hour for the complete replication of a mtDNA molecule, and approx. 5 days for half the mitochondria in primate tissues to be replaced. Thus, if the number of DNA molecules replicated during a given time is increased, then the rate of mutation for that DNA will theoretically be higher. Brown et. al. (1979) state that the rate of evolution of a molecule is equal to the product of the rate at which new mutations arise multiplied by the fraction of these new mutations that are eventually fixed. Wilson et al. (1985) believe that both of these factors are elevated for mtDNA, thereby, resulting in a more rapid evolution in mtDNA (five to ten times faster) than in nuclear DNA.

While these are reasons for believing that the mutation rate is elevated in mtDNA, it also seems likely that a greater fraction of mtDNA mutations can be tolerated or fixed in tRNA and rRNA genes due to relaxed constraints on the translational apparatus, since mtDNA encodes only 13 polypeptides, (none of which is directly involved with its own replication, transcription or translation). Thus, less accuracy is more selectively tolerable in a small system that synthesizes only 13 kinds of polypeptide chains

Despite its high rate of evolution, mtDNA remains a very conservative molecule and will mutate on average only over several hundred generations. An individual's mtDNA will normally be almost identical to its mother, maternal grandmother, maternal great-grandmother etc. By measuring the number of mutations that have occured between two individuals and estimating the rate at which those mutations arose, it would be possible to trace back to a point at which they both shared a common ancestor. In order to determine an individual's or a population's ancestry, the genetic diversity in mitochondria of present human populations must be measured. This procedure involves specific laboratory techniques and requires a number of underlying assumptions that are discussed in the following section.

8.2.3. Methodology

MtDNA is easily isolated and purified in the laboratory compared to nuclear DNA which requires more elaborate technological expertise. There are two techniques used by geneticists to isolate and purify mtDNA.

a.) Restriction enzymes

Although restriction enzymes provide only an indirect way of observing DNA sequences, it is the most commonly used method for determining the differences between samples of human mtDNA. The technique is based on the use of specific enzymes which recognize a specific sequence length of four to six base pairs. The enzymes cleave or cut the DNA whenever the particular sequence is seen, thereby producing a pattern of fragments. The occurence of a mutation or change in the base pair will cause an alteration of a specific sequence and the restriction enzymes will not recognize the new pattern.

The collection of fragments produced by a restriction enzyme is analyzed by separating the fragments using electrophoresis. This technique moves the restriction fragments through an electrical force gradient and separates the proteins by charge and by size. The rate of migration depends on the net charge on the restriction fragment which will depend on its nucleotide length and its base composition. The fragments are then detected by using one of three procedures:

1) direct staining (with ethidium bromide), or

2) Southern blotting followed by hybridization with a radioactive labelled DNA probe whereby only DNA fragments containing sequences homologous to the probe will be observable, or

3)attaching radioactive phosphate to the ends of the fragments prior to electrophoresis.

For the last two methods the fragment patterns are then visualized by autoradiography (x-ray). The use of radioactive probes is necessary only in nuclear DNA, because a typical digest will cleave mtDNA in only a few places, producing only a few fragments. The fragments themselves can thus be radioactively labeled and visualized by exposure to X-ray.

The resulting variations in DNA fragment lengths are called "restriction fragment length polymorphisms" (RFLPs). A map of the fragments, known as a restriction map, is produced, which reflects the linear arrangement of selected nucleotide sequences in designated regions of the genome. A comparison of the restriction maps from related organisms gives an estimate of the number of nucleotide substitutions per site. This estimate is subsequently utilized in statistical formulae to give an estimate of the degree of sequence divergencve.

Each of these methods has various benefits and problems. The main advantage of the Southern blotting method is that it is not necessary to use purified mtDNA and requires only blood samples, since the method of detection depends on hybridization with a specific mtDNA probe. The other two methods require mtDNA that has been purified from placentas by ulatracentrifugation (Brown 1979). The longer purification process, greater degree of technical knowledge and the need for placental doners causes major constraints on the total sample size. However, the benefit of Southern blotting technique is outweighed by the fact that type of restriction enzyme used results in relatively few, larger fragments because fragments that are less than 250 basepairs in size cannot be detected. Therefore, within a sample population using Southern blotting method it is not possible to distinquish between mtDNAs that differ by less than 0.5 percent. The other two methods using purified mtDNA can use electrophoretic techniques that resolve much smaller fragments, thereby differentiating mtDNAs that differ by 0.1 - 0.05 percent. The third method, radioactive end-labelling technique, has the greatest resolving power and requires the least amount of purified DNA.

After the fragments produced by restriction enzymes are separated by electrophoresis and detected by one of the three methods mentioned above, the fragment patterns (restriction map) can be compared to the pattern from a complete, published sequence known from one individual (Anderson et al. 1981). In this way, the location of mutations causing different fragment patterns can be inferred and the frequency of mutations across the mtDNA genome can be anlyzed.

The main problem in using restriction enzymes is that they reveal only a fraction of the total number of mtDNA mutations, Therefore, it is necessary to use a combination of many enzymes that detect many sites. Often differences in interpretation between various studies can be ascribed to the lower resolving power of one study over another (Cann et al. 1987, Stoneking and Cann 1989).

b.) Sequence Analysis

This second technique for mtDNA isolation and purification is superior to restriction enzyme analysis because sequencing permits the detection of all the mutations within the part of the genome that is being observed. Thereby, maximum resolution of mtDNA types can be detected.

Up until very recently, sequence analysis required the cloning of mtDNA into a plasmid or viral vector. This procedure is very time-consuming and requires high technical expertise. A new technique called Polymerase Chain Reaction (PCR) negates these problems.

PCR is a technique for the enzymic synthesis of a DNA segment, whereby the exact sequence to be amplified is specified by two primers,(short molecules of single-stranded DNA designed to match opposite ends of the two complementary strands of the target DNA), bounding the fragment to be replicated. Repeated cycles of denaturation, annealing and extension of the segment, result in the exponential accumulation of the sample DNA that can then be sequenced by conventional techniques. The PCR method can be applied to extremely small quantities of mtDNA resulting in a thousand-fold amplification of the specific target DNA region over a very short period of time i.e only a few hours.

Recent studies show that PCR is an essential tool for the analysis of ancient DNA, as it can be used for degraded and chemically modified DNA samples (Paabo et al. 1989. The oldest tissue from which useful sequences have been recovered is from a Magnolia leaf dating approximately 20 million years ago (Golenberg et al. 1990). Fragments of DNA from blood samples (Wrischnik et al. 1987), single hairs (Higuchi et al. 1988), mummified human remains (Paabo et al. 1989) or ancient skeletal remains (Horai et al 1989) can be used as a template to make more DNA. Therefore, the use of PCR can provide significant phylogenetic information from ancient tissues preserved in frozen, dry, or water-logged environments (Hagelberg et al. 1991).

Another problem in the analysis of DNA sequences, for the purpose of comparison between two populations, is that only a tiny fraction of the three billion nucleotides of the human genome has been sequenced. However, DNA sequence data, when available in sufficient quantity, should, in time, prove useful for human genetic distance studies.

8.2.4. Individual Sequence Variation

Before 1979, attempts to measure genetic variation and distance have been based on the products of nuclear genes such as blood groups, serum proteins, and red cell enzymes etc. These traditional studies have used gene frequncies as comparisons between population groups. In contrast, mtDNA estimates of genetic variation and distance are based on accumulated sequence divergence and thus reflect the actual number of nucleotide substitutions that have occurred between mtDNA molecules in individuals or in population groups.

The sequence divergence between each pair of mtDNA types can be estimated from the restriction maps and averaged over all pairs to obtain an estimate of mean sequence divergence within a population (i.e. the mean number of nucleotide substitutions per base pair observed per pair of individuals. Genetic distance between two populations can be estimated by the mean sequence divergence of pairs of mtDNAs involving one individual from each population (corrected for mean sequence divergence within each population (Wilson et al. 1985, Cann et al. 1987).

8.3. MT.DNA STUDIES OF HUMAN ORIGINS

Using the theoretical and methodological perspective outlined above, Cann et al. (1987) and Stoneking and Cann (1989) have provided genetic evidence for a recent African origin for all modern humans. Utilizing the restriction enzyme method, they mapped approx. 9% (coding and non-coding samples) of the mt.DNA from the placentas of 147 humans from Africa, Asia, Australia, New Guinea and Europe. They found that mtDNA diversity (or greatest number of mutational changes) is higher in humans with African ancestry than any other geographic region. The phylogenetic tree constructed from the resulting 133 mtDNA types revealed two major clusters: one entirely African and one mixed African/non-African. They concluded that Africans have been diversifying longer than any other population and that Africa was the homeland of modern humans.

Furthermore, utilizing a mutation rate of 2-4% per million years, Cann estimated that the common ancestor of all modern mtDNA types lived between 140,000 and 280,000 years ago. Also, the ancestral stock of all Eurasians separated from an African stock between 90,000 and 180,000 B.P. Since mtDNA diversity is relatively low in Eurasian populations, Cann sugests that hybridization between archaic humans and modern humans was essentially nil, because, if there was hybridization between archaic Asian groups and anatomically modern groups migrating from Africa, "we should expect to find extremely divergent types of mtDNA in present-day Asians" (Cann et al. 1987:35). Since these divergent types do not occur, either there was no hybridization or, there may be additional factors influencing mtDNA variability. It is this very issue, regarding factors causing mtDNA variability, that has resulted in heated arguments against Cann's theoretical perspective. In the following chapter I detail the problems with the underlying assumptions used by Cann and colleagues in their argument for the worldwide replacement of archaic *Homo sapiens* by a new species of modern *Homo sapiens sapiens*.

CHAPTER 9. PROBLEMS IN THE REPLACEMENT MODEL

While supporters of the Replacement Model argue that the genetic evidence is accurate, all geneticists do not agree with the interpretation of these results, or the reliability of the data, or the constancy of the molecular clock. Initial arguments against Cann's genetic data include the use of assumptions that may be unfounded. For example:

1. The SAMPLE SIZE is relatively SMALL.

Considering that 133 different types have been found in 145 individuals, more types may exist worldwide, but have not yet been detected. Therefore, other studies of larger groups may provide more variable types in non-African populations. Also, the sample size of DNA fragments is small. That is, an average of 370 nucleotide bases per individual were surveyed, which represents about 9% of the 16,569 nucleotide bases in the mitochondrial genome. Excoffier et al. (1989, Morris 1992:141) argue that the very small sample sizes chosen by Cann severely underestimate the mtDNA variability. They suggest that in any other classicial genetic marker study, these samples would have been rejected.

2. They assume that most MUTATIONS ARE NEUTRAL.

Cann states that most mutations occur in noncoding regions of the DNA, or do not cause amino acid substitutions and are therefore probably neutral in their effect on the phenotype. If they are neutral, then their occurrence and accumulation are a function of time, that is, the more variable a group is, the older it is. She states that since African groups are the most variable, they must be the oldest.

It is true that the measure of variability is based on the number of mutations which differentiate groups. However, SOME types may possess a selective advantage. Recent studies (Spuhler 1988) suggest that a significant portion of the mt. genome is under strong selective constraints. There may be as much selection acting on mtDNA as on nuclear DNA. One study on *Drosophila* suggests that selection acting on either mtDNA or nuclear DNA can influence each other (MacRae and Anderson 1988 cited in Wolpoff 1992:29). In addition, the high incidence of transitions produces parallel and back mutations at the same site among lineages. Clearly, the assumption of complete mtDNA neutrality is incorrect.

3. They assume that mutations accumulate at a CONSTANT RATE.

The estimate of when the common ancestor lived is based on the certainty of the rate of mutation. The estimate of this rate is based on choosing a group that colonized an area at a defined time and then remained isolated. The time for accumulated mutations is then estimated. The groups chosen for this purpose are those that colonized New Guinea at 30,000 B.P., Australia at 40,000 B.P., and the New World at 12,000 B.P. These estimates result in a divergence rate of 2-4% per million years. This rate suggests that initial divergence occurred between 140,000-290,000 years ago.

However, bottlenecks or genetic admixture can alter the distribution of lineages and thus the amount of variability. Such bottlenecks and admixture occurred in Australia, New Guinea and the New World, with all three regions peopled by two or more major migrations. Spuhler states a bottleneck could result in the loss of all mt.DNA variability. Therefore, this factor affects the estimate of the rate of mutations, which in turn affects the degree of divergence, which in turn affects when the common ancestor lived. Thus, all of Cann's assumptions are based on previously unfounded assumptions.

In addition, the mutation rate of 2-4% is based on a divergence time of 5 million years between humans and chimps. However, if earlier divergence dates of 9 mya are used, the rate for hominids becomes 0.5 - 1% per million years (Brown 1985). Other studies by Nei (1985) derive a divergence rate of 0.71%, which is based on a divergence time of 13 mya for *Pongo*, and suggests a chimp-human divergence of 6 million years ago. This slower rate indicates a divergence time for modern humans of approximately 850,000 years ago, a time when *Homo erectus* was first leaving Africa.

Spuhler's (1988) data indicates that many mtDNA types are very old in regions outside of Africa and that their ancestry can be extended beyond Cann's estimates. Excoffier and Langaney (1989) argue there is great time depth and regional variation to existing mtDNA. They find that most of the differentiated mtDNA types in Africans "have appeared only recently" (Excoffier and Langaney 1989:82). They also conclude that selection may have played a role in mtDNA evolution and that the genealogical tree used by Cann is biased by topological errors.

The initial discovery of limited mtDNA variability in human populations led almost immediately to the simplest or most parsimonius explanation; i.e. assuming that random mutations are the main source of variation, the small number of variants indicat a short time span of mutation accumulation and thus a recent origin for modern humans. Alternatively, Avise et al. (1984), Spuhler (1988) and Wolpoff 1989, 1992) argue that the low mtDNA variability of humans may be explained by other factors. For example, via the process of stochastic lineage extinction all existing mitochondria variants will eventually become extinct. That is, due to its haploid inheritance, mtDNA lineages may become extinct as a result of random chance. Under most conditions the stochastic extinction of mt. lineages (like the extinction of surnames) will be rapid, and the chances of a lineage remaining extant indefinitely are relatively small. Using surnames analagously to mtDNA, Yasuda et al. (cited in Smith 1989:57) studied the extinction of surnames in a population over a period of 300 years (10 generations) and found that about 80% of the male lineages initiated by a single male became extinct. Wolpoff (1992) concludes that random loss (i.e. differential lineage survivorship), rather than ancestry from a single source population, is almost certainly the cause of the mitochondrial pattern of limited variation.

When Avise et al. (1984) examined the variables affecting the rate of stochastic lineage extinction, they found that in a stable population of n females it is highly probable that within 4n generations all of the descendants will trace their common ancestor to a single female founder. Another variable identified by Avise was the relationship between population growth and lineage extinction. A population decreasing in size will have rapid lineage extinction. Alternatively, a population expanding in size will result in higher probability that two or more lineages will survive.

Cann et al. (1987) argue that the low diversity found in mtDNA of present-day humans is not the result of lineage extinction because the Pleistocene African populations were expanding. However, while population expansion during the Holocene was dramatic, this may not have been true during the Pleistocene when human groups may have been growing minimally, or not at all.

Latorre et al. (1986) refute the "Mother Eve" hypothesis in their study of mtDNA variation of a fly species that is widely distributed in the Old World, but has only recently migrated to the New World and expanded dramatically.

They forecast that flies studied at a future time, thousands of years hence, may all have mtDNA that had been derived from one specific morph. However, the speculation that they were all descendents of one ancestor is fellacious, since this morph is found in 44% of the present-day population. Moreover, individuals with the same morph would carry the nuclear DNA of inumerable ancestors. Similarly, although all modern humans MAY share a common ancestral mt.DNA type, their NUCLEAR DNA comes from ancestors that need not have been African, and may even have been archaic *Homo sapiens*. Latorre et al. (1986) adds that, at present, there is "no convincing evidence that mtDNA evolves like a molecular clock, at rates that would persist from one group of organisms to another, or over long evolutionary spans" (1986:8652). Rather, the discrepancy of rates based on different data suggests that mutation rates may change over time and between organisms.

Further criticisms of Cann's analysis include the use of restriction analysis, which is an indirect method of comparing mtDNAs, instead of the direct method of sequence comparison. Also, Cann's study was based on a large sample of African Americans instead of native Africans. Furthermore, she used an inferior method (i.e. midpoint method) for placing the common mtDNA ancestor, instead of using the outgroup method.

Recently, in an attempt to address several of the weaknesses of Cann's original study, Vigilant et al. (1991) expanded the sample size and utilized more rigorous hypothesis testing in her study. Using sequence analysis instead of restriction enzyme analysis, and the outgroup method instead of the midpoint method, in addition to a sample of native Africans, Vigilant concluded that their results were supportive of Cann's African origin hypothesis. This detailed study seemed to solidify the Eve hypothesis more firmly into a theoretical framework.

However, an apparently fatal flaw in Cann's and Vigilant's statistical analysis may have ended the idea of an African Eve. Templeton (1992) argues that the computer program used by the group is procedurally faulty and statistically flawed. Ironically, the problem is "maximum parsimony", or the supposition that the best hypothesis is the simplest one with the least assumptions. Applied to nucleotide sequences, the most parsimonious solutions are those with the smallest numbers of base changes. When this information is entered into a computer programme (called Phylogentic Analysis Using Parsimony or PAUP), it strives to find the most parsimonious tree, the one with the minimum number of mutations. This "shortest path" is considered most likely to reflect evolutionary processes. After each computer run several possible trees are offered; then the researcher must choose how many computer runs to do, and how many thousands of trees to save after each run for later analysis. The researchers using PAUP drew their conclusions after examining 100 trees from only a single run. It is argued that they should NOT have stopped at 100 because that is a nonrandom sample of trees that are considered equally parsimonious by the program. Furthermore, Vigilant's data were entered in sequence, allowing the trees to be built up as the program runs. But simple sequence addition is unsuitable for large data sets, which should be entered at random with many runs performed to achieve consensus. When entered at random, the number of possible phylogenetic trees is larger than 1 billion and would accommodate all possible homelands for humanity (Templeton 1992).

Not surprisingly, there is no dispute that African mtDNA is, indeed, more diverse than that from other geographic areas and may thereby reflect a more ancient origin for humanity than posited by the Eve hypothesis. Thus, the mtDNA data is highly problematic in its assumptions and requires further research before it can be utilized to resolve questions of modern human origins. Based on the available mtDNA data, the Replacement Model is not supported by the genetic evidence. Nonetheless, genetic studies are capable of being very useful to answer questions regarding more recent migration patterns and population affinities, as discussed in the following chapter. Furthermore, the potential for the isolation and study of ancient nuclear DNA is a fascinating possibility for future research.

CHAPTER 10. POTENTIAL OF MT.DNA AND NUCLEAR DNA MARKERS

While the mtDNA studies mentioned in the previous chapters are highly problematic in determining the origins of modern humans, there is nonetheless a great potential for nuclear and mt. DNA genetic analyses that are capable of providing substantive evidence for human migrations and inter-relationships between major geographic populations. Following are examples of different genetic studies indicating the relationships between various groups.

Stoneking and Wilson (1989b), state the loss of one of two copies of a 9 base-pair repeated sequence in a small noncoding region of the mtDNA appears to be a marker for populations of Asian origin. They have shown that the deletion occurs in coastal P.N.G., Melanesia, and is nearly fixed in Polynesia, but it is absent from Australia and the highlands of New Guinea. This distribution of the deletion might reflect a relatively recent migration of people through the South Pacific, after the complete separation of the Australian and New Guinea land masses approx. 6000 years ago. The geographic isolation of the New Guinea highlands could account for the absence of the deletion there, but it is not clear why people with the deletion would not have reached Australia, since they crossed much larger expanses of ocean between Polynesian islands. One possible explanation is that the route of colonization of the people with the deletion was through northeastern Indonesia, along the coast of New

Guinea, and then out to Melanesia and Polynesia. If so, the deletion should be present in northeastern Indonesia (eg. the Moluccas) but not in southeastern Indonesia (eg. the Nusa Tengarra chain of islands). Stoneking and Wilson screened 146 individuals from two islands in the Moluccas and four islands in the Nusa Tengarras for the presence of the deletion. The deletion was present in all six Indonesian populations, with the frequency ranging from 8% to 32%; the frequency was not significantly higher in the Moluccan populations. The absence of the deletion in Australia thus remains an enigma.

Another example regarding the potential of mtDNA is the research by the Japanese team of Saitou and Harihara (1989) which has integrated and analyzed previously available data from studies that have been published for various populations. Phylogenetic relationships of mt.DNA types were analyzed for 885 individuals from 15 different populations. Those included were Caucasian, Chinese, Bantu, Bushman, Japanese, Ainu, Korean, Negrito of the Philippines, Vedda of Sri Lanka, Amerindian, Tharu of Nepal, Roman and Sardinian of Italy, and Jew and Arab of Israel. All the individuals were classified into 57 types by combining four restrictions enzymes. The unrooted tree thus obtained has the following characteristics:

1) African populations are far apart from the remaining populations.

2) Mongoloids in the broad sense are closely related.

3) Caucasoid populations are located between African and Mongoloid populations.

4) Vedda is located between Mongoloid and Caucasoid populations.

Another study by Cavalli-Sforza (1991), has mapped the worldwide distribution of hundreds of genes from which he inferred the lines of descent of populations and compared them to linguistic groups. He found that the genetic distances between Africans and non-Africans exceed those found in other intercontinental comparisons. The genetic distance between Africans and non-Africans is roughly twice that between Australians and Asians, and the latter is more than twice that between Europeans and Asians. i.e. 100,000 years between Africans and Asians, 50,000 between Asians and Australians and 40,000 years between Asians and Europeans.

Wainscoat et.al. (1989), using the distribution of Alpha and Beta Globin gene cluster polymorphisms, also found a major division of humans into an African and a Eurasian group.

Lucotte (1989)) discusses evidence from the Y-chromosome and the attempts to elaborate the paternal ancestry of modern humans. He suggests that the data so far favour an early split between African and Eurasian pop's, but are not sufficient, to reach any statistical significance.

Rouhani (1989) analyzes mitochondrial DNA trees, nuclear DNA trees, enzymes and blood groups and concludes that although the genetic studies show a division into two major groups - Africans and non-Africans, the evidence is nonetheless controversial and the extent of intercontinental gene flow and its implications remain unresolved.

Ryk Ward (1989) examines the implications for the peopling of the Americas. Sequencing of a 360 nucleotide segment of the mt. control region for 63 individuals from the Nuu-Chah-Nulth (Nootka) of the Pacific Northwest, revealed the existence of 28 lineages defined by 26 variable positions. This represents a substantial level of mt. diversity for a small local population. Furthermore, the sequence diversity among these lineages is over 60% of the mt. diversity observed in major ethnic groups such as Japanese or Sub-Saharan Africans. It was also observed that the majority of the mt. lineages of the Nuu-Chah-Nulth fell into phylogenetic clusters. The magnitude of the sequence difference between the lineage clusters suggests that their origin predates the entry of humans into the Americas. Since a single Amerindian tribe can contain such extensive molecular diversity, it is unnecessary to presume that substantial genetic bottlenecks occurred during the formation of contemporary ethnic groups. In particular, this data does not support the concept of a dramatic founder effect during the peopling of the Americas.

Another study by Schell and Blumberg (1988) analyzes the potential of genetic studies in order to resolve questions of population origins. They have determined that two variants of albumin can connect New world and Old World tribes by analyzing the locus for the albumin gene which is on chromosome 4. This chromosome is one of the best-mapped human chromosomes. Variants of serum albumin are known from populations around the world, and since 1955 more than 60 albumin variants have been named. Albumin Naskapi is most common among the Indians of Quebec, in whom the gene reaches frequencies of 13%. It is also found at high frequency among Athabascan speakers such as the Navajos and Apache of Arizona, in addition to other Athabascan speakers from Alberta and Alaska. Based on archeological and glotto-chronological analyses, Athabascan groups are believed to have reached the southwest approx. A.D. 500 after a gradual migration from the north. The presence of albumin Naskap among the southern Athabascans reflects, on a biologic level, their past history and cultural relationship with the northern Athabascans. Albumin Naskapi has also been discovered in a population of Turks and perhaps among Indians of the Punjab in north India. It was shown that the amino acid substitution was identical in the Turkish and North American samples. The presence of albumin Naskapi in these Asian groups identifies them as remotely related to American Indians.

The second type of albumin variant called albumin

Mexico extends from the southwest United States to Mexico's northern Gulf Coast and as far south as Guatemala City. This distribution parallels archaeological evidence of past relationships among Mesoamerican cultures. The presence of albumin Mexico in the Guatemalan highlands and its absence from the Yucatan are consistent with archeological evidence of the pattern of influence from the Valley of Mexico. To the north, the distribution of albumin Mexico also parallels the area of influence from the Valley of Mexico. Archeological evidence indicates that this influence may have reached the U.S southwest, and the Hohokam culture in particular.

A study by Serjeantson (1989) on the Human Leucocyte Antigens (HLA) indicates genetic affinities between Southeast Asian populations. HLA are coded on Chromosome 6 and expressed on the cells of all tissues. They are highly variable with distinctive features and able to provide information on population origins and affinities. It was found that:

1. P.N.G. Highlanders and Australians have common ancestry of great antiquity. Highlanders originated with a very small population and have since been totally isolated from their Melanesian neighbours.
2. P.N.G. coastal populations and island Melanesians are very similar in HLA distributions. These distributions suggest that Proto-Polynesians probably coexisted with Melanesians.

3. HLA system shows little contact between Polynesians and Melanesians.

4. Early Austronesian voyagers did not carry Melanesian genetic elements into eastern Polynesia. Antigens not represented in the migrating groups suggest Eastern Polynesia was colonized by a small number of settlers. Also, Maoris, Hawaiians, and Easter Islanders are part of the eastern Polynesian Branch, while Maoris and Hawaiians split from each other 1000 B.P.

5. The possiblity of a minor Amerindian contribution to eastern Polynesian cannot be excluded. However, this affinity is of great antiquity, prior to eastward colonization of the Pacific.

Chromosome 6 also has complement proteins coded by genes in the Histocompatibility complex. They are involved in the immune response, but are serum blood proteins rather than cell surface antigens (as in the previous study). These proteins are highly variable and potentially useful in revealing similarities/differences between populations and in tracing origins/ migrations. In a study of the genetic variants of the serum complement components, Ranford (1989) illustrates the close genetic relationship between Chinese, Japanese, Koreans and Thais. He also finds that Melanesians and Micronesians are similar but Northern and Central Australian Aborigines are different from each other and also different from Asians and Pacific Islanders. He suggests genetic diversity between Northern and Central Aborigines may be due to migrations by genetically different people or else may be due to divergent evolution by tribes isolated for long periods.

Genetic variants of haemoglobin (Hb) are abundant, easily analysized and have been widely surveyed in all human ethnic groups. The degree of geographic endemicity of malaria is correlated with the geographic variation in the thalassaemia gene, thereby supporting the hypothesis that the gene for thalassaemia provides some protection from malaria. In thalassaemia frequencies, coastal P.N.G. pop's differ strikingly from Highland populations, but not in their other Hb gene markers, probably due to malaria selective forces (Hill 1989). Hb data show no support for any close relationship between Melanesians and African populations, although globin gene data argue very strongly for Mongoloid and Melanesian ancestry in the Polynesian gene pool. Micronesians have been the least studied, but evidence for large S.E. Asian or Mongoloid genetic connection exists between Micronesia and Polynesia (Hill 1989).

Serjeantsom and Hill (1989:286), in a study on the origins of the Pre-Polynesians, argue that extreme views suggesting that Polynesians evolved within Melanesia from a group existing there for 30,000 years is unsupported by genetic data. All of these genetic data indicate the seperate identity of P.N.G. Highlanders from the coastal populations. This suggests a small number of founders, and no flow of genes into the Highlands. However, genetic evidence is equivocal regarding the question of a single or dual colonization of Australia.

Several recent studies have shown disparities when comparing genetic distances using different types of genetic loci. Results based on blood groups (red cell antigens) and actual DNA sequences often show an apparent lack of agreement. This may be partially explained by the influence of natural selection on blood groups, the complex dominance relationships among blood group alleles, and the poor understanding of the relationship between red cell antigens and DNA sequences. Also, many of the problems presently observed in genetic distance studies reflect a paucity of appropriate data rather than deficiencies in methodology (Jorde 1985). This problem underscores again the need to employ as many loci as possible in genetic distance studies.

Clearly, new DNA studies and technologies are only beginning to yield a mass of potential information. In particular, the potential for the analysis of ancient DNA is astounding. As mentioned previously, the oldest tissue from which useful sequences have been recovered is from a Magnolia leaf dating approximately 20 million years ago (Golenberg et al. 1990). Also, fragments of DNA from blood samples (Wrischnik et al. 1987), single hairs (Higuchi et al. 1988), mummified human remains (Paabo et al. 1989) or ancient skeletal remains (Horai et al 1989) can be used as a template to make more DNA. However, only a few tiny segments out of a total of three billion bases of the genome have been examined by DNA techniques, thus, a need for further studies is paramount. Also, little is known about the factors affecting DNA preservation and recovery. While studies have shown that genetic information can be recovered from archaeological and forensic bones (Hagelberg et al. 1991), little work has been done to determine how environmental conditions such as depth of burial or soil pH may affect DNA survival.

Thus, the need for wide-ranging comparative genetic studies from many populations is essential before it is possible to determine origins, colonization sequence, and when/where significant bottlenecks occurred. Nuclear DNA and mitochondrial DNA can augment more traditional morphological, behavioural and fossil-based research, and together with the integrated efforts from multiple disciplines, progress can be made.

CHAPTER 11. PROBLEMS IN TAXONOMIC METHODOLOGY

The question of human evolution cannot be discussed without elaborating on the limitations of taxonomic methods used by scientists to determine the evolutionary history or phylogeny of a species.

Systematics, or taxonomy, is the scientific study of the kinds and diversity of organisms and of any and all relationships among them (Simpson 1964). In order to reconstruct the phylogeny of a species, systematists make inferences based on observational and experimental data that appear to be relevant. They use one of four major approaches to this question: classical evolutionary taxonomy; phenetics; cladistics; or molecular taxonomy.

11.1. CLASSICAL EVOLUTIONARY TAXONOMY

Classical evolutionary taxonomy (also called evolutionary systematics or classical systematics) is the most popular approach and depends, more than any other, on the experience and subjective judgment of the observer. The methodology requires the examination of as many independent traits or characters of a species as possible to determine the differences and similarities of a species. By using many different types of traits, it is assumed that misleading data from any single trait will be observed by a lack of agreement with the data from other traits. The traits most easily studied and widely used are those pertaining to morphological comparisons between living and fossil forms. The classical approach, therefore, is based on evaluating similarites within a wide range of traits.

However, similarity, by itself, does not necessarily indicate common evolutionary descent. A particular similarity may merely reflect a similar adaptation to the same environmental stress. Convergent evolution occurs when organisms that are not closely related become more similar in certain traits because of independent adaptation to similar environmental conditions. Thus, when classical systematists find similarities between two species, they must determine whether they are homologous (inherited from a common ancestor) or analogous (similar in function and structure, but of different evolutionary origins).

The problem with this methodology is the utilization of intuitive personal judgment in deciding which traits should be considered and how they should be weighted. This unusual degree of subjectivity has motivated the use of phenetics, a method that was considered to be relatively more objective by taxonomists.

11.2. PHENETICS

Phenetics, also called numerical taxonomy, was more popular during the 70's than it is at the present time. It is based solely on the degree of phenetic (observable) similarity between different organisms. It is an approach that uses as many traits as possible, all of which are weighted equally and ignores the issue of analogy versus homology. The assumption is that if enough traits are compared, any errors will be cancelled out or swamped by the mass of other data.

Phenetics, however, makes two assumptions that are questionable. First, it assumes that all characters are equally useful in determining phylogeny, and second that little convergent evolution has occurred. In fact, these two assumptions are often invalid. The premise that any large sampling of traits would reflect phylogeny, is incorrect, since similar phenotypic linkages have no necessary link to biological reality, especially when there has been no discrimination between homology and analogy.

11.3. CLADISTICS

Cladistics has become a common method of taxonomic classification since Hennig's work on phylogenetic systematics in the 1960's. Both the Replacement and Continuity Models use this methodology in their attempts to delineate differences or similarities between fossil remains. However, cladistics has limitations that are seldom considered when applied to the hominid fossil record.

In the jargon of cladistic analysis, the homologies (structural similarities due to inheritance from a common ancestor) that are shared by closely related taxa are called synapomorphic traits or shared, derived traits. Homologies from a more remote ancester are called symplesiomorphic traits or shared ancestral traits. The traits that are unique to a specific taxon are called autapomorphic traits. The focus is on shared derived characters (synapomorphies) or traits that are common to the species and are of relatively recent instead of ancient origin. Thus, in cladistics, traits shared in general would not be considered, while a phenetic approach would use any measurable trait. Cladists weight equally each of the traits they consider, but by ignoring features presumed to be shared at the point at which the speciation occurred, they can be more selective than phenticists. However, deciding what traits are shared, derived characters still calls for subjective judgment. Cladistic analysis, like phenetics, assumes that analogous traits will be outnumbered by homologous ones, thereby, assuming that false similarities will not distort the analysis. However, interpretations based on this assumption can cause unreliable and inaccurate conclusions.

The most common way to distinguish apomorphic (derived) traits from plesiomorphic (primitive) ones is to compare the frequency of the occurrence of specific traits in a number of closely related taxa or outgroup (eg. African apes are outgroup for Hominidae). The assumption is that the most frequently occurring traits, in a wide group of taxa, will be those that were present in the common ancestor. This technique to determine the direction of a trait is called determining the polarity of the morphocline. The morphocline is the sequence reflecting the probable pathway of changing traits. The decision regarding whether a trait is primitive or advanced is the most controversial area in evolutionary analysis today, because there is often disagreement regarding the inferred direction of change. Although the outgroup comparison is the most reliable way of establishing the polarity of a morphocline, it frequently produces conflicting results when different traits are introduced into the analysis or when different researchers carry out the analysis. Also, the degree of evolution within the outgroup's lineage since the common ancestor existed, is often unknown.

Another way of determining the polarity of the morphocline (identifying ancestral character states) is by comparing the fossil record for the earliest ontogenetic traits because those traits that develop earliest in an individual may also be ancestral to the species. However, it is not always reliable to assume that the particular traits found in a fossil is necessarily primitive in relation to the trait observed in a later species because fossil species can be very specialized in their traits.

A further problem within the cladistic approach is that studies of the origin of anatomically modern humans using a strictly cladistic approach is inappropriate because it takes too narrow a view of morphology by requiring only the notation of the presence or absence of a trait. Thereby, cladistics does not allow for morphological variation (Trinkaus 1990, 1992; Habgood 1989).

Also, cladistics is problematic in accounting for mosaic evolution, whereby different traits may change at different rates, because cladistics assumes that traits change in consistent ways through time. Cladistic classifications are also inherently unstable because the reclassification of a single trait from an inferred advanced state to an inferred primitive state, due to the discovery of a new fossil, can result in major changes to the cladogram. For these reasons cladistic classifications often fail to mirror evolutionary descent.

Further limitations include the uncritical assumption of parsimony, or the assumption that the simplest explanation is the most likely one. Although the principle of parsimony is a useful tool for the generation of testable interpretations of given data sets, it is often taken as a true representation of the real world. Parsimony is only an optimization model, a mathematically derived theoretical ideal which assumes that the simplest solution has the greatest probability of accurately representing the real world. In fact, however, it is not a true aspect of biology and can never be more than an approximation of reality (Trinkaus 1990,1992) For example, parsimony relates directly to the identification of homoplasies and software programs such as PAUP (Phylogenetic Analysis Using Parsimony) are capable of identifying possible homoplasies mathematically. Yet, most appropriate developmental comparisons are possible only for neonotological material, and they are rarely available through the fossil record. Consequently, most identifications of homoplasies are the products of mathematical computations, not of biological evaluations of the given traits. Furthermore, all Homo populations share a broad biological baseline upon which evolutionary processes operated. It is likely, that similar evolutionary pressures on allopatric populations sharing similar biology will probably produce similar morphologies independently. Thus, despite the geographical distance between African and Asian *H. erectus* it should not be surprising that *H. erectus* from the two regions would show parallel evolutionary trends given their similar basic adaptive patterns and common ancestry. It is, therefore, unlikely that we can determine possible homoplasies from closely related groups (Trinkaus 1990:4).

Another issue that has not been addressed is the biological relevance of the traits employed. The problem is that many of the shared derived traits are of unknown or minor functional significance. It is unknown to what extent different traits may be intercorrelated. Are we identifying the primary biological features or merely a secondary reflection? For example, in the cranium, alteration in one feature can have consequences for other aspects of this complex functional unit. As a result, the identification of primary biological traits, as opposed to traits that are secondary consequences, will influence the number and polarities of the perceived traits (Trinkaus 1990). In this way traits that are evolving in tandem, are often treated as separate traits, thereby tending to inflate the importance of what may actually be only one phenomenon (Skelton cited in Habgood 1989:245). This problem is exemplified by the disputable interpretations regarding the number of traits that separate Asian and African *Homo erectus*. Stringer has proposed TWLEVE derived traits separating these two *Homo erectus* populations, whereas Wood quotes SIX traits and Andrews quotes FOUR. In contrast, Hublin has proposed that most of these derived features are related to an increased bony mass of the vault and suggests that these traits can be combined into ONE derived trait -- bony hypertrophy. Clearly, the identification of the independence of traits MUST precede their interpretation. Unfortunately, few comparative studies attempt to address this issue.

Finally, the attempts to define modern *Homo sapiens* within a taxonomic system also remain ambiguous. Day and Stringer (1982) have provided specific criteria for applying their definition of modern humans to fossil remains. They utilize six criteria which include: a short but high crania, a high frontal bone that lacks a continuous supraorbital torus, a long and high parietal arch that is inferiorly narrow and superiorly broad, and an occipital bone that is well curved, rather than angulated in the sagittal plane. The criterion is that over 50 percent of the preserved cranial traits in a specimen must be "modern" for it to be considered anatomically modern. Using these criteria, Wolpoff (1992) applied them to living Aboriginal populations of Australia. He found the existence of many modern individuals, including females, possess measurements that are outside the range of modern *Homo sapiens* as defined by Day and Stringer. Wolpoff (1992) also tested a recent prehistoric sample of Australian Aborigines from the Murray Valley at the sites of Coobool Crossing and Kow Swamp, dated to the early Holocene. He did not include known gracile specimens from Lake Mungo, nor extremely robust specimens such as Cossack, Mossigiel, and WLH 50. Out of 31 adult crania, 9 (or 29 percent) were NOT anatomically modern according to Day and Stringer's criteria, even though all of these specimens, living and prehistoric are obviously modern. Also, artificially deformed crania (Brown 19981) were found to be included in the "*Homo sapiens*" definition. Wolpoff makes two conclusions; first, the regional morphology of Australiasa is not a consequence of artificial deformation, as expressed by other researchers (Stringer and Andrews 1988), and secondly the definition of modern *Homo sapiens* (Day and Stringer 1982) is unreliable.

Therefore, as a classificatory system, cladistics may be advantageous in allowing a more explicit definition of morphological criteria, however, based on the above examples, it relies upon assumptions that cannot be substantiated and may result in incorrect phylogenies.

11.4. MOLECULAR TAXONOMY

The fourth method of classification is called molecular taxonomy. This approach avoids the analogy/homology issue of specific traits and focuses instead on the molecular level. Since neutral base changes (those that do not significantly alter the activity of the gene product) are thought to accumulate at a relatively constant frequency, the number of neutral differences between equivalent gene sequences in two species is a rough measure of the time since they had a common ancestor. However, as discussed in Chapter 9, this assumption is also problematical, considering the uncertainty of factors affecting the rate of mutation changes.

Nonetheless, molecular taxonomy has already helped systematists resolve traditionally controversial questions. For example, it was found that classical taxonomists had correctly put the species of Tasmanian wolf in the same line as the Australian marsupial carnivores, whereas cladists had mistakenly classified it with a group of South American marsupials. It is possible that molecular taxonomy may replace cladistics as the most popular alternative to classical taxonomy, especially if some of the DNA of extinct forms is adequately preserved. Despite this possibility, DNA typing from ancient bones is far from being a routine technique because at the present time, little is known about the factors affecting DNA preservation and recovery (Hagelberg et al. 1991).

11.5 MORPHOLOGY AND SPECIATION

Besides the problems that have been discussed regarding the use of various taxonomic methods, there is a dilemma regarding the most basic assumption for fossil species designation: i.e. the assumption that species differences are correlated to morphological change. All traditional taxonomic methods use morphological criteria as the most important component in species definitions. However, with the increasing application of chromosomal techniques to living populations, data has emerged that effectively falsifies these taxonomic assumptions. It has been found that differences in morphology DO NOT necessarily delineate a seperate species, and vice versa, that extensive speciation can occur with little morphological change (Lambert and Paterson 1982, Tattersall 1986). This statement is paradoxical to paleoanthropologists, who utilize morphological discontinuity as exclusive criteria for determining specificity. As such, the varying degrees of morphological change which can characterize speciation (from none to marked) presents an astounding obstacle to the consistent and objective designation of fossil species. Even in those examples where morphological discontinuity and speciation can be shown to coincide, the fundamental problem of homoplasy can still confound the investigator.

Therefore, the inherent assumptions that exist within traditional taxonomic methods must be continually questioned because they are heavily weighted by inconsistent and subjective judgement. The solution lies not in further elaboration of traditional methodologies which are based on morphological criteria, but on future genetic comparative data that may allow paleoanthropologists and biologists to understand, in greater detail, the relationship between morphology and speciation.

CONCLUSIONS AND FUTURE RESEARCH

Clearly, neither of the two models UNEQUIVOCALLY explains the available data at the present time. Both the Continuity Model and the Replacement Model have weaknesses and limitations in their theoretical perspectivies and methodological analyses. I believe the genetic evidence used by supporters of the Replacement Model is highly problematic in its methodology, does not adequately explain the data, and is based on underlying assumptions that are invalid. Additionally, the chronometric evidence for replacement remains questionable and subject to serious errors. Alternatively, the Continuity Model also has insufficient technological and faunal data and is limited by the extensive gaps between the latest archaic and earliest modern specimens in Southeast Asia. Thereby, the Continuity Model has been unable to determine the constancy of regional traits. However, the Continuity Model, from its perspective, is best able to explain the present data and support its underlying predictions for transitional fossils, particularly in China and to a lesser degree in Indonesia and Australia. Furthermore, a more solidly based model will not be achieved without the integrated efforts of many related disciplines. Each group has tended in the past to keep to its side of a disciplinary divide, or too often, have uncritically used each other's work.

Therefore, in response to the initial six queries in this thesis, future research must include resolutions to the following issues before a final model can be constructed:

Question 1. Was there technological continuity or change in peripheral geographic regions such as China and Indonesia during the Upper and Middle Pleistocene?
Answer - The Chinese technological record indicates a gradual *in situ* evolution of increasing complexity throughout the Pleistocene, but with the chopper/chopping tool industry remaining a major component of all lithic assemblages. A sudden change in technological/cultural behaviour patterns reflecting replacement by a new people with superior technological skills is not noted by researchers in China. Even the Bamboo-Karst model, initially formulated by Pope (1982), suggests that specialized tools utilized in China during the middle and late Pleistocene, may have occurred in the form of a non-lithic, geographically-contained bamboo industry that was not available in the West.

In Indonesia the absence of a lithic record that is clearly associated with *Homo erectus* makes it difficult to allow correlations with Chinese technological assemblages. Previous attempts to connect Chinese technocomplexes to the Javanese Pacitanean industry have been negated by controversy regarding stratigraphic correlations, lithic typologies and theoretical biases. Future work must include the re-analysis of depositional sequences in order to allow for the possibility of association of artifacts with skeletal remains of *Homo erectus* and early *Homo sapiens*. Considering the difficulty of separating convoluted strata within such a tectonically volatile and highly eroded geographic area, this goal is daunting to geologists and archaeologists alike.

Question 2. Did paleoecological factors prevent or contribute to faunal/hominid migrations into China and Indonesia?
Answer - Periodic land bridges between many islands of southeast Asia, were sufficiently extensive to allow faunal/hominid routes from China to Indonesia during the Pliestocene. However, previous analyses of faunal structures are now considered to be out of date and based on insufficient data. Presently, there is doubt regarding the high degree of isolation that existed for faunal groups within China. Even the presence of a separate Sino-Malayan and Siva-Malayan Faunal structure is now in doubt. In fact, faunal differences may be based more on a latitudinal separation than on a geographic, regional separation. Thus, a re-analysis of von Koenigswald's faunal correlations is necessary before it is possible to determine the degree of isolation between these two regions.

Question 3. Is there evidence for morphological continuity or replacement in regions of China, Indonesia or Australia?

Answer - Phylogenetic affinities between Asian *Homo erectus* and living Mongolians may be substantiated by evidence for regional traits that continue in high frequency in both archaic and modern populations within China. Also, in Australasia, there may be morphological evidence for affinities between Indonesian *Homo erectus* and modern Australian aborigines. However, there is continuing debate on the relevance of regional morphological traits to determine hominid evolutionary sequences. Both models accept the fact that all of the earliest modern humans from each geographic area in South Africa, Central Europe and Southeast Asia exhibit archaic-type traits, reflecting their descent from archaic forerunners. The controversy continues to lay within the basic question: are these archaic-type traits primitive retentions from a single ancestral *Homo sapiens* population, or are they transitional traits reflecting gradual, worldwide *in situ* evolution? Some data has suggested that a combination of specific traits (related to facial flatness in China, and facial prognathism/frontal angulation in Australasia) occurs in a higher frequency in these respective areas than other regions throughout the world. However, the question regarding the validity of transitional specimens, cannot be resolved until the chronometric data for South African/Eurasian early modern sites and Southeast Asian late archaic sites can be more precisely delineated.

Question 4. How reliable is the context and dating evidence for the earliest anatomically modern sites in South Africa?

Answer - At the present time the types of dating techniques used at all three of the South African early modern sites are considered imprecise or experimental and contain a wide error range. Uranium series dates have been obtained from KRMS while it has been argued that uranium contamination exists within the zone of ground water percolation!! The stratigraphic context from Border Cave is subject to a degree of uncertainty because of the possibility of intrusion of the fossils into a lower level. Also, at Omo, attempts to determine number of years that have passed based on thickness of a deposit is too imprecise on which to provide a specific date for the earliest modern humans. The KRMS, Border Cave and Omo hominids lie outside the range of conventional radiocarbon dating, meaning they are minimally 40-50,000 years old, IF one is willing to accept radiocarbon dates on mollusc shell.

Question 5. How valid are the assumptions used by mtDNA research to suggest replacement of archaic humans on a worldwide scale?

Answer - Several of the assumptions are founded on previously unfounded assumptions, such as the neutrality of mutations and the accumulation of mutations at a constant rate. Also, the suggestion that limited mtDNA variability in modern populations is a reflection of a small, relatively recent founder group from Africa denies the additional factors that may cause low mtDNA variability such as random lineage extinction and forces of natural selection.

Therefore, mutation rates of mtDNA must be quantified using mtDNA from fossil skeletons of known age in order to determine the exact rate of change over time. Also, the sample size must be vastly increased, both in number of people sampled worldwide, and number of nucleotide bases tested. Additionaly, the use of continuing nuclear DNA studies, such as those discussed in Chapter 10, can provide complementary data to mtDNA studies in order to determine population origins, migrations and affinities.

Question 6. How do we recognize species in the fossil record?

Answer - While problems of fossil species designation remain arbitrary, the question of modern species designation within any of the classificatory systems remains problematic and subjective. For many modern Australian crania, morphological definitions of modern *Homo sapiens* has resulted in their exclusion from the taxon!! The lack of knowledge regarding the extent of functionally correlated traits tends to dilute any conclusions that may be forthcoming. The assumption that species differences are correlated to morphological change has also been questioned by geneticists. Extensive speciation can occur with little morpholgical change, or vice versa, differences in morphology do not always delineate a separate species. The use of morphological discontinuity as exclusive criteria for determining species differentiation can no longer be utilized when examining fossil specimens. Thus, classificatory systems presently utilized require us to make certain assumptions that cannot be substantiated, and forces us to place data into categories which can obscure and distort information of evolutionary relevance.

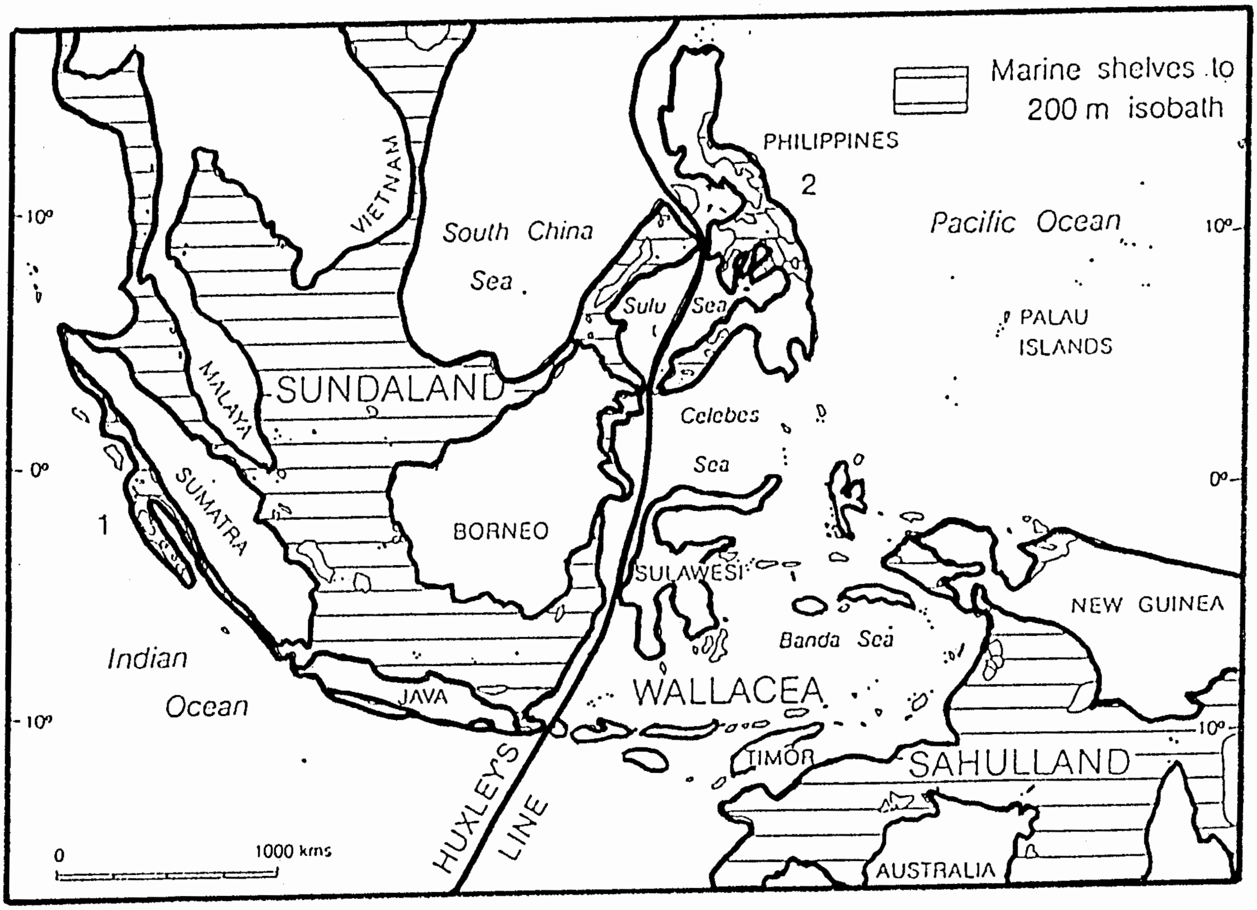
In conclusion, in an attempt to re-focus on the factors involved in modern human origins, I would like to stress that all the traits marking the differences between archaic and modern *Homo sapiens* are merely in the degree of phenotypic expression within a variable species. I suspect that cranial and post-cranial robusticity are part of a complex of interrelated traits that are controlled by changes in the regulatory part of the genome. A change in the control mechanism of bone growth (hyperostosis) could cause both facial reduction, and decreased skeletal robusticity, both of which mark the difference between archaic and modern humans. This change in the control mechanism would be adaptively selected for under conditions of reduced stress that lessened the need for bone robusticity. Such conditions existed during the Middle Paleolithic when climatic amelioration and technological innovations reduced the adaptive advantage for robusticity. This regulatory shift would NOT entail a speciation event, because the allelic change would gradually spread throughout the population for whom it was beneficial. Therefore, those populations who did not utilize technological innovations, or did not experience climatic amelioration, would not be adaptively selected for decreased bone robusticity. Eventually, however, as all Late Paleolithic cultures began to utilize the newer technological innovations, sufficient gene flow between regions would have allowed the spread of the regulatory allele change.

A relationship between enviromental stress, mutations and evolutionary change can be substantiated by genetic studies of retroviral-like DNA (Retroviral-like Transposable Elements or RLE's). The insertion of viral-like DNA segments may bring about rapid and dramatic changes in gene regulation and development, and may contribute to the major organismic-level changes that characterize macroevolution. The mutation rate of retroviruses (and RLE's) can be induced by environmental stress such as radiation, viral infection, thermal and chemical stress. Stress-induced increases in mutation rates have been shown to rise in bacteria that are subjected to environmental stress (MacDonald 1990). It is surprising that the significance of a stress-responsive mutation system has had little impact on evolutionary theory, despite the fact that its potential importance has been repeatedly noted. Because major bursts of morphological diversity, as recorded in the fossil record are usually associated with ecologically stressful conditions, stress-induced mutations may be important in generating morphological diversity (MacDonald 1990:188). It is concluded that major organismic-level changes that characterize macroevoluton may have their genetic basis in changes occurring at regulatory loci which control development.

A final solution to this question is not possible, however, until we are able to understand the inter-relationship between DNA, morphological change and environmental stress. I believe it is the feed-back relationship between this triad that will ultimately explain the more detailed factors involved in organismic speciation events and evolutionary processes.

Figure 1.

Map of Indonesia (Sunda and Sahul)



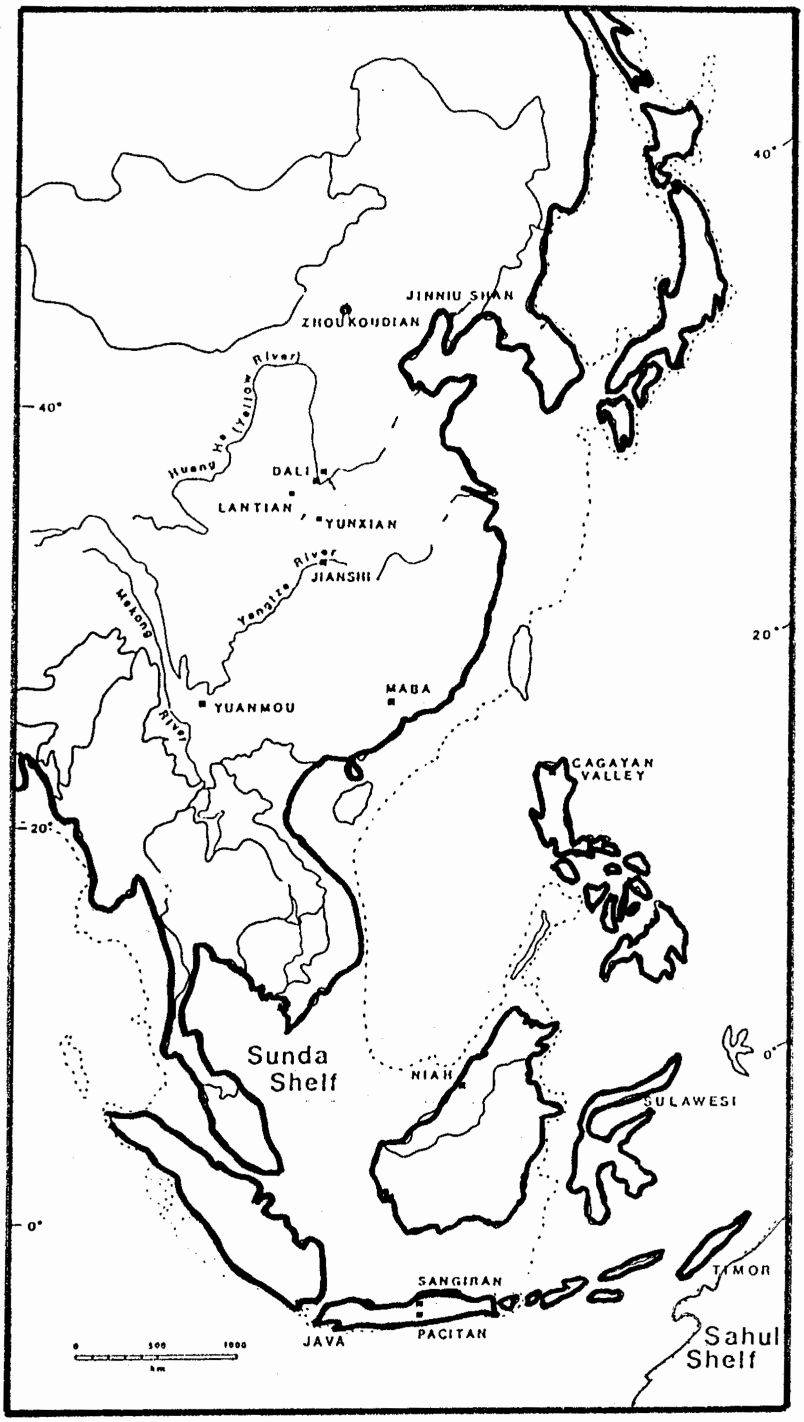


Figure 2. Map of Chinese Sites

Figure 3. Map of Australian Sites.

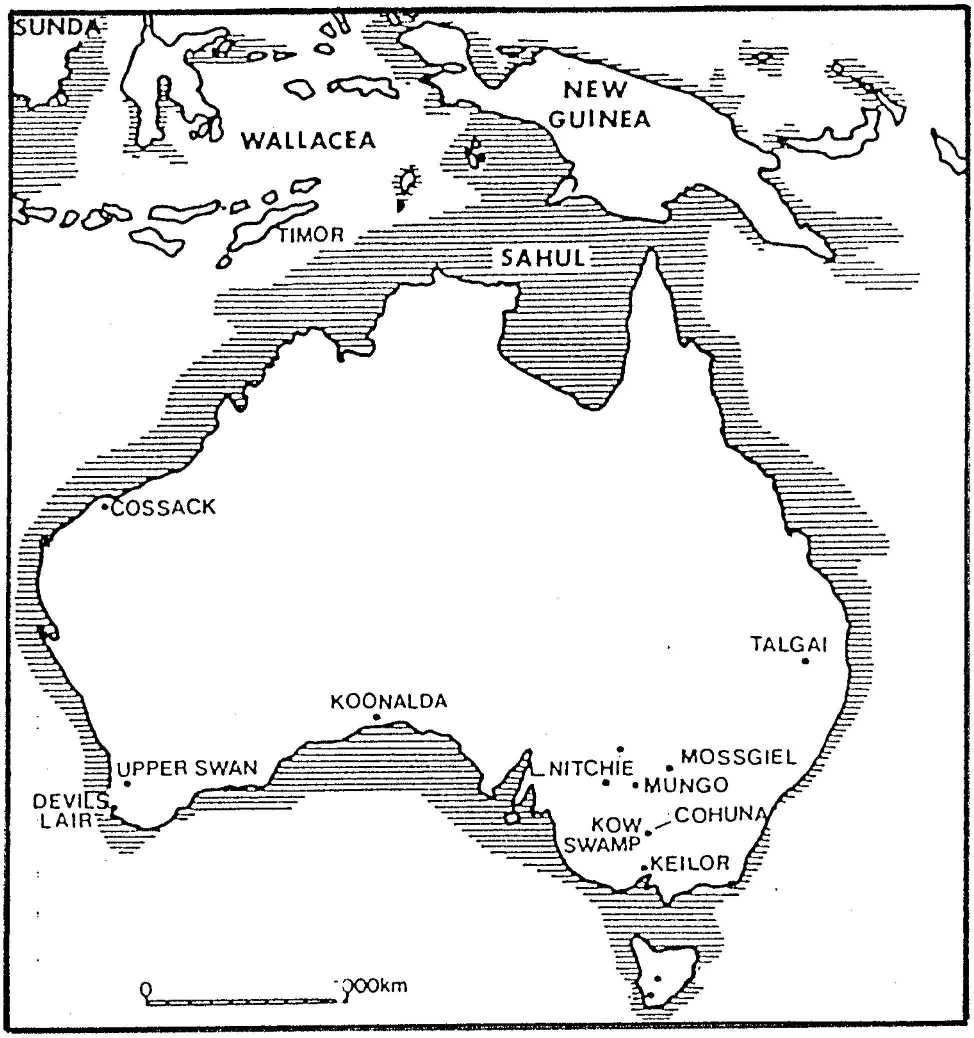


Figure 4. Map of African Sites.

(courtesy: H. Odwak)

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