## Investigation into the presence of purported lineage continuity in Australasia

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# INVESTIGATION INTO THE PRESENCE OF PURPORTED LINEAGE CONTINUITY IN AUSTRALASIA 

## By

Peter Ferdinando

A Thesis Submitied to the Faculty of<br>The Dorothy F. Schmidt College of Arts and Letters<br>In Partial Fulfillment of the Requirements for the Degree of<br>Master of Arts

Florida Atlantic University
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# INVESTIGATION INTO THE PRESENCE OF PURPORTED LINEAGE <br> CONTINUITY IN AUSTRALASIA 

## By

## Peter Ferdinand

This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Doug Broadfield, Department of Anthropology, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Dorothy F. Schmidt College of Arts and Letters and was accepted in partial fulfillment of the requirements for the degree of Master of Arts.

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|  | Abstract |
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The debate concerning the appearance of modern humans is currently divided into proponents for Multiregional continuity and advocates for a Replacement of all archaic hominin populations by a single, African source. Australasia has been touted as the best evidence for continuity. Utilizing a review of the purported morphological basis of this continuity, it is clear that the proposed unique Australasian features are primitive retentions from Homo erectus. However, African-derived modern humans lack these traits. Consequently, the only group from where these features could be acquired is Indonesian Homo erectus. Henceforth, there appears to be a combination of a discrete African origin for the modern Homo sapiens morphology and limited interbreeding that generates the archaic features present in modern human fossil specimens from Australia. It would seems probable that the interactions of Homo sapiens and Homo erectus in Indonesia may have paralleled those of modern humans and the Neanderthals in Europe.

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## Chapter 1—Introduction

## Theoretical Background

In the recent literature, two major hypotheses have developed to account for the appearance and global occupation of modern humans. The Recent African Origin (RAO) model believes that Homo heidelbergensis (also known as archäic Homo sapiens) developed into modern Homo sapiens in only one location, which was most likely Africa. Subsequently, Homo sapiens spread to the rest of the planet replacing existing populations of archaic humans (Stringer and Andrews, 1988). The Multiregional Evolution (MRE) model asserts that earlier regional populations evolved into modern humans through a complex process of genetic exchange, with retained regional features from their archaic ancestors (Thorne and Wolpoff, 1981; Wolpoff et al., 1984). In addition, there are weaker versions of each theory, which allow for both an African origin and archaic/modern intermixing.

RAO emerged in its current form with a seminal article by Stinger and Andrews (1988), although Stringer had been working towards this concept for many years (see Stringer 1994 for his personal history of RAO development). This, though, was not the first assertion of a single continental origin; Louis Leakey (1963) posited an origin in Africa during the 1960's. RAO claims that modern Homo sapiens evolved in Africa alone and then colonized and replaced existing populations of Homo neanderthalensis in Europe, Homo heidelbergensis in China, and Homo erectus ini Indonesia (Stringer and Andrews, 1988; Stringer, 1992b; Stringer and McKie, 1996). This theory is based on a
combination of fossil evidence, DNA interpretation and the spread/replacement of culture and technology.

The fossil evidence puts the emergence of modern humans as early as 130 kya (from the Omo-Kibish site), but the generally accepted date is about 100kya to 70 kya (based on finds from Border Cave and Klasies River Mouth) (Stringer, 1992b; Stringer and McKie, 1996). RAO asserts that the earliest specimens of modern humans are from Africa. While the earliest African fossils are fragmentary, several series of finds from the Middle East bolster the RAO position. This is because the clearly modern Skhul and Qafzeh specimens, which date to about 90kya, predate the latest European Neanderthals and Indonesian Homo erectus, proving that neither of these two groups can be directly ancestral to modern humans. In fact, Homo sapiens appears relatively late in Europe, and Australasia, demonstrating a spread and replacement from Africa, rather than a global evolution through gene flow. Also, there are no good transitional fossils between modern and archaic humans in any region except Africa. Furthermore, RAO contends that many of the Multiregional proposed features that link modern human regional groups to ancestors from non-African regions are also present in the earliest African moderns. Therefore, these regional traits are retained from an African origin, not from archaic regional populations.

The emergence of modern genetic examination during the 1980's formed the basis for the current incarnation of the RAO theory (see Stoneking et al., 1986; Cann et al., 1987; Stoneking and Cann, 1989). Stinger and Andrew (1988) focused on several different examples to demonstrate a recent, African origin. First, they reviewed the lack of variation in both the mitochondrial and nuclear DNA of modern humans, when
compared to other hominoids like chimpanzees. This lack of diversity is purported to show a lack of temporal depth for Homo sapiens. In addition, the lack of variety in mtDNA has revealed a possible bottleneck in human evolution, where very few individuals existed. This bottleneck implies that it was not possible for there to be genetic connections between the widely scattered populations of the Old World. Furthermore, this bottleneck may have allowed for the biological speciation of Homo sapiens before their renewed expansion out of Africa (Brauer and Stringer, 1997; Stringer and McKie, 1997). Second, the greater genetic diversity in Africa reveals a longer time of separation between African groups relative to non-Africans. This is linked with the fact that African mtDNA has two branches; one that leads to every other regional group and one that is purely African. In addition, an assumed, constant accumulation of mtDNA mutations allowed Stringer and Andrews (1988) to pinpoint the origins of genetically modern humans between 140,000 and 290,000 years ago. The assumption of a consistent mutation rate is controversial (see Wolpoff, 1989; Frayer et al., 1993; and Templeton, 1993), but this point has been re-enforced and complimented by further genetic research on mtDNA and nuclear DNA along with work on the $Y$ chromosome and the recent sequencing of fragments of Neanderthal mtDNA (see Stringer and McKie, 1996; Brauer and Stringer, 1997; Krings et al., 1997; Jorde et al., 1998, Underhill et al., 2001).

A final line of evidence for RAO is the spread and replacement of cultures, especially tool technology and art. This is clearly evident in Europe with the abrupt emergence and spread of the Upper Paleolithic tool industries (Aiello, 1993). Starting about 40,000 years ago the established Neanderthal Middle Paleolithic (Mousterian) tool
tradition is replaced by the Upper Paleolithic (Aurignacian, Perigordian, Gravettian, Solutrean and Magdalenian) tool industries, the latter has been mainly associated with modern humans. Interestingly, several of the late Neanderthal sites, which date after modern human entry into Europe, have tool traditions (Chatelperronian and Uluzzian) that appear to have been influenced by the Upper Paleolithic tools (Harold, 1989; Mellars, 1989, 1999; Stringer, 1992b; Vandermeersch, 1997). The above evidence clearly demonstrates the lack of direct continuity between Neanderthals and Homo sapiens in Europe. If modern humans emerged in Europe, there should be a clear developmental relationship between the presumed ancestor/descendant's cultural heritage; there is not. However, this evidence does not negate possible hybridization between these two species. Unfortunately, a cultural sequence of the clarity found in Europe is not currently present in other areas of the Old World (see Wolpoff et al., 1994 for a suggestion that the little cultural and technological evidence that has been recovered from Asia supports the MRE perspective).

The major issue in RAO is that modern humans from Africa replaced the already established archaic populations in the rest of the Old World. Generally, it is believed that replacement was either total, and thus no gene flow occurred between the two populations, or the mixing of these populations was small enough to produce little effect on modern Homo sapiens (Stringer, 1992a). There is some disagreement over the amount of gene flow that was possible between the archaic and modern human groups. Gunter Brauer (1992) has posited an idea entitled the African Hybridization and Replacement (AHR) model that is an offshoot of the main RAO theory. This model considers that an African replacement was primary, but because modern humans were not
a distinct species there could have been some interbreeding between them and archaic populations (Brauer, 1992). AHR specifically allows for intermixing, but seems to downplay the importance of gene flow in the appearance of modern humans.

The idea of a nearly complete replacement appears to be supported by two of the above lines of evidence. First, the lack of genetic diversity among humans and analyses of both mitochondrial and nuclear DNA lends strong support to a recent origin of modern humans. Second, replacement, as recognized by the spread of new technologies, has been proven in Europe by the substitution of the established Neanderthal tool traditions. The major problem for RAO is morphologically based. The initial modern human fossils from Africa are incomplete and the author believes that there is a strong possibility of gene flow between Homo sapiens and Homo neanderthalensis in Europe, from Chinese Homo erectus through Chinese Homo heidelbergensis into modern Chinese and between modern humans and late Homo erectus in Java. This claim is based on some morphological similarities, which appear to represent non-African regional continuity. These morphological potentials are the basis for the Multiregional theory.

Multiregional Evolution proposes that human regional variation, which originally occurred when Homo erectus emerged from Africa to populate the Old World, has been continued into modern Homo sapiens (Thorne and Wolpoff, 1981; Wolpoff et al., 1984). This theory emphasizes morphological traits that persist in non-African regions from archaic populations into Homo sapiens and is based on observed continuity of regional traits in fossils from Northern Asia, Australasia and Europe. It does not suggest multiple origins for each of the regional populations of Homo sapiens.

MRE has two central tenants, which initially appear paradoxical. There is an empkasis on variation among regions, which is seen by the presence of unique combinations of regional traits. Therefore, evolution should, through time depth, result in the speciation of these distinct regional groups. Conversely, in recent human evolution there is clearly a species-wide evolutionary trend towards the features of modern humans. Thus, there is a force for regional selection of distinct traits and a force that unites the species. The former, regional continuity, was recognized by Franz Weidenreich in the 1940's, but the latter, gene flow, was not documented until the publication of the theoretical background for MRE in the early 1980's. This second force allows for the exchange of genetic material betwein regions and prevents total speciation. MRE posits that humans are a species with great morphological variation, because there are several adaptive crests in human features as you move through different environments (Wolpoff, 1989). This is the resolution to the conflict between local, regional selection and worldwide, species selection.

Earlier it was stated that the weakest evidence for RAO was based on morphology, the converse is true for the Multiregional viewpoint. Morphological data provides the foundation for MRE and was the impetus for the formation of this theory (see Wolpoff and Caspari, 1997). MRE has attempted to demonstrate regional continuity in Europe, Australasia and China. The suggested continuity traits for the Australasian region are central to this thesis and are reviewed later in this chapter. The idea of a regional continuity in North Asia, especially China, has a basis in the work of Franz Weidenreich. He asserts that there are twelve traits that link modern Asians to Chinese Homo erectus (Weidenreich, 1943). In Europe, Fred Smith (1984) has focused attention
on traits that he believes could link late Neanderthals to early modern humans. He does caution that the continuation of Neanderthal traits in modern humans does not necessarily mean that modern Europeans are only descended from Neanderthals. For each of the above regions, many authors have observed a combination of traits that appears to establish a degree of regional continuity (Thorne and Wolpoff, 1981, 1992; Wolpoff et al., 1984, 1994; Smith, 1984, 1992a; Habgood, 1985, 1989; Wolpoff, 1985, 1989, 1992; Smith et al., 1989; Brauer, 1992; Aiello, 1993; Frayer et al., 1993; Hawks et al., 2000), while others (Stringer and Andrews, 1988; Groves, 1989a; Stringer, 1992a; Lahr, 1994; Brauer and Stringer, 1997; Brown, 2000) believe that these proposed traits are either the result of a different phenomena other than continuity, or do not represent a particular region, even in combination.

In addition to the morphological evidence, MRE theorists use limited genetic data to support their viewpoint. Supporters provide examples of nuclear and mtDNA that is purported to show either the lack of a bottleneck, or that some modern humans have genes that are present in other regions, but not in Africa (Frayer, 1993; Jorde et al., 1998; Adcock et al., 2000). They also cite that the mtDNA evidence used by the RAO theory is flawed, because 'the calibration of any mitochondrial clock has major accuracy problems" (Frayer, 1993:40). Multiregionalists claimed that if the mtDNA mutation rate is calibrated to the paleontological evidence of the divergence of chimpanzees and humans, then the clock used by Cann et al. (1987) is too fast. According to MRE, a new recalibrated rate derives a common ancestor at about 850̂kya (Wolpoff, 1989). This date was further refined and pushed back to 1.3mya (Wolpoff et al., 1994). Both these dates could correspond to a migration of Homo erectus out of Africa, but could not relate to the
migration of modern humans. Moreover, Stringer and McKie (1996) have pointed out a major problem with these new calibrations. There is a four million year gap between current estimates of human/chimpanzee split. Thus, any mtDNA date can be manipulated depending on the divergence date that is used.

Similar to Brauer's AHR theory, there is a less stringent concept that emphasizes regional continuity, but does believe there can be an almost complete genetic origin of modern humans from Africa. Smith (1989) has developed this idea, which is entitled the Assimilation Model (AM). The AM asserts that there is a combination of an African origin and continuity between non-African regional populations (Smith et al., 1989). This model implicitly allows for intermixing between archaic and modern groups, which explains the continuity traits, but consents to an almost complete African origin for the modern pattern of morphology, which encompasses the genetic evidence.

## The Concept of the Continuity Trait

This volume analyzes the validity of the Multiregional concept of continuity traits. To clearly pursue these proposed regional traits through the fossil record there must be an essential part to this evaluation of the literature. That element is the history and the identification of these proposed continuity traits. Without an unambiguous understanding of this concept this analysis cannot proceed.

Regional continuity of traits was defined by Wolpoff (1999:811) as
"[T]he observation that there is a sequence of anatomical features, often found together, spanning the time from earlier to later populations in a geographic region, that seems to reflect some degree of ancestral-descendant relationship."

The current interpretation of MRE uses combinations of regional traits to demonstrate ancestor/descendent relationships between modern Europeans and Homo neanderthalensis, modern Australians and Javanese Homo erectus, and modern Chinese through Chinese Homo heidelbergensis to Chinese Homo erectus. It is important to remember that these traits are used in combinations, not as isolated traits. Also, MRE does not posit a multiple origins concept, all human groups were connected by gene flow.

The latter point from the above paragraph is of great importance and should be reaffirmed. The MRE perspective asserts that all humans are one species. While they trace specific region combinations, each region's modern humans are just as advanced as those from every other area. This position has been emphasized because both Franz Weidenreich's ideas, and the later Multiregional theory have been misconstrued as suggesting multiple origins and a parallel evolution for Homo sapiens. This mischaracterization adds Multiregionalism as a component of Polygenic theory. Polygenism states that each race is significantly different, possibly at the species level.

This idea has extremely negative racial consequences and has been vigorously denounced by the MRE theorists (Wolpoff and Caspari, 1997b; Wolpoff et al., 2000).

Franz Weidenreich $(1943,1949)$ first popularized the idea of the continuity traits. First, he asserted morphological similarities between the earlier and later Homo erectus specimens from Java. Second, he linked later Indonesian Homo erectus from Ngandong to the Australian Aborigines. This feat was accomplished by a list of seven features that are reprinted in table 1-1. Weidenreich developed one of the central tenants of the current MRE theory, the temporal depth of regional traits, but his work did not include a second essential point; just how humans stayed untied as a species if regional traits were developing? This question remained unanswered for nearly forty years.

It is with sadness to note that Weidenreich was preparing a monograph specifically focused on the human remains from Ngandong, but he died before its completion. This book, entitled Morphology of Solo Man, was published in 1951 and contains his unfinished manuscript. His earlier work asserted that he saw a rather direct line from earlier Javanese Homo erectus through later Javanese Homo erectus to modern Australians (Weidenreich, 1943). Larnach and Macintosh (1974) stated that his view had subtly altered before his death. He now believed that the Ngandong fossils only had a partial role in the origin of the Australians, but he did not state where else this origin might have been from.

Weidenreich introduced the Australasian pillar of MRE, but he also demonstrated a realization of the limitations and dangers of using such continuity traits. First, he understood that the traits he used to link Ngandong and the Aborigines are not exclusive to these fossils. It has been repeatedly stated by the advocates of the Multiregional theory
that their concept analyzes a combination of regional traits, not individual features. Many of the traits that make up these regional combinations can be found as isolated, individual features in populations other than the specified region. Second, while he did not have a workable mechanism for it, Weidenreich (1946) asserted the unity of humans. Even though he recognized specific regional groups, he believed that all humans were a single species. This comment may seem commonplace today, but during Weidenreich's life people were still debating if "Linnaeus' species Homo sapiens refers only to the white man" (Weidenreich, 1946:1).

Carleton Coon expanded Weidenreich's observations in his 1962 book The Origin of Races. While Weidenreich and the later MRE theorists took great pains to clearly state that they did not believe there were unique origins for each of the human races, Coon has been accused of not making this distinction clear. It is not apparent if he truly was an overt racist (a story related in Stringer and McKie 1996 seems to indicate this may have been the case), but his work could easily be misinterpreted. When the book was published a storm of criticism was leveled at Coon and he was relegated to the backwaters of academia (Dobzhansky et al., 1963; Stringer and McKie, 1996). The Origin of Races was published during one of the most turbulent time in United States history, and Coon's conclusions were used by several different groups to legitimize segregation and discrimination against African Americans. This work cast a negative shadow on the concept of continuity traits. This blemish would not be truly lifted until the early 1980's and the emergence of the Multiregional Theory.

Larnach and Macintosh (1974) tested the assertion that modern Australians could be linked to Indonesian Homo erectus. Their review of the continuity traits for the

Australasian region is especially important, because they reveal Weidenreich's altered perception of the origin of the Australians. Weidenreich's later viewpoint is closer to Smith's AM concept and relates to the contribution of an archaic source into a modern population. Larnach and Macintosh (1974) defined eighteen features found on the Ngandong specimens, then analyzed their frequency in modern populations. Their results clearly showed the Ngandong population could not be directly ancestral to modern Australians, but it was possible that some interbreeding may have occurred. It is the latter idea that this thesis is directly concerned with studying. Their trait list is reproduced in table 1-2.

Dealing with the Australasian region, Multiregional theory has several trait lists that can be evaluated. Before the publication of a general Multiregional theory in 1984, Alan Thorne and Milford Wolpoff (1981) had recognized thirteen traits, which linked Indonesian Homo erectus to the late Pleistocene modern humans from Kow Swamp in Australia. These are replicated in table 1-3. In their 1984 publication, Wolpoff, Thorne and Xin Zhi asserted fourteen continuity features, reproduced in table 1-4. They described nine features that are general similarities between Indonesian Homo erectus and modern Australians and five traits that directly links modern Australians to late Homo erectus from Ngandong.

The following four tables represent the proposed Australasian continuity features that have been discussed over the last half a century.

Table 1-1 Weidenreich (1949)-Links between Ngandong and Australia

1) Well-developed superciliary ridges-This is usually called a supra-orbital torus, or a browridge. There is a clear bar of bone over the eyes, formed by extension of the frontal.
2) A flat, far-receding forehead-This is a common trait found in Homo erectus, Homo heidelbergensis and Homo neanderthalensis. The frontal is a lot more horizontal in orientation giving the skull a clearly different shape then modern human crania.
3) A prelambda depression-There is the presence of a slight dip at the midline between the parietals immediately before they join the occipital at the lambdoid suture.
4) A torus-like demarcation line between occipital and nuchal planes-This is the presence of a crest of bone across the occipital just above the nuchal lines where the neck muscles attach.
5) A sharp bend between the upper and lower scales of the occipital bone-This trait is linked with 4), due to the presence of an occipital torus the upper part of the occipital is rounded in shape as it leads into the torus, where-as the lower part of the occipital is angled almost horizontal as it move up to the torus.
6) The pterion region reveals a short sphenopariteal articulation ( $5-8 \mathrm{~mm}$ )-This feature will not be used due to the inability to see it on the casts and photographs. 7) The infraglabellar notch is deep and narrow-This is the presence of a deep groove between the medial part of the inferior portion of the supra-orbital torus and the nasal aperture.

Table 1-2 Larnach and Macintosh (1974)-Characteristics of Solo (Ngandong) Man

1) Brow ridges are of the divided type-The presence of a supra-orbital over both orbits.
2) A very large rounded zygomatic trigone is present-The zygomatic bone is flared out
on Sangiran 17, where-as a modern one tends to sweep straight back. This feature will not be used because it is only preserved on one specimen and this is not from the temporally late Ngandong series.
3) A distinct ophrionic groove-A dip in the supra-orbital torus at the glabella, or at the mid-point above the nasal aperture.
4) A suprameatal tegmen-The presence of a shelf of bone over the external auditory meatus.
5) The long diameter of the external auditory meatus is horizontal-The modern external auditory meatus is longest in the vertical axis, where-as the Ngandong specimens have a large, horizontally angled external auditory meatus.
6) The tympanic is orientated horizontally and is convex-- This feature will not be used due to the inability to see it on the casts and photographs.
7) The squamous suture is low, with practically no arch-This feature is due to the receding frontal, the temporal/parietal suture is almost horizontally straight, where-as in moderns this suture is much more curved.
8) The course of the squamo-tympanic fissure is transverse-This feature will not be used due to the inability to see it on the casts and photographs.
9) The squamo-tympanic fissure is on the floor of the glenoid fossa-This feature will not be used due to the inability to see it on the casts and photographs.
10) The postglenoid tubercle is absent-This feature will not be used due to the inability to see it on the casts and photographs.
11) Weidenreich's spina cristae petrosae is present-This feature will not be used due to the inability to see it on the casts and photographs.
12) The petrous portion of the petro-tympanic axis is clearly angled forward in relation to the tympanic portion-This feature will not be used due to the inability to see it on the casts and photographs
13) The foramen ovale is situated at the bottom of an oval pit-This trait is inside the skull, thus this feature will not be used due to the inability to see it on the casts and photographs.
14) A juxtamastoid ridge-This feature will not be used due to the inability to see it on the casts and photographs.
15) A lamdoidal protuberabce-Right after the prelambda depression the occipital is slightly higher than the parietal.
16) A large ridge-shaped torus-This is the presence of a crest of bone across the occipital just above the nuchal lines where the neck muscles attach.
17) A strong external occipital crest emerging from the midline of the occipital torus and extending downward towards the foramen magnum-The underside of the occipital torus is well developed.
18) A marked sulcus supratoralis is present-The presence of a dip between the supra-orbital torus and the upward sweep of the frontal.

Table 1-3 Thorne and Wolpoff (1981)-Indonesian Grade Similarities

1) Vault proportions-This trait is excluded because it is extremely vague and the vault proportions are the result of the combination of the features covered below.
2) Continuity of the supraorbital torus across the midline-Where the browridge continues above the nose.
3) The presence of a broad continuous sulcus separating the torus from frontal squama-A dip in the supra-orbital torus at the glabella, or at the mid-point above the nasal aperture.
4) Marked post-orbital constriction-The frontal sharply narrows behind the eyes.
5) The presence of an angular torus-A clear line on the parietals between the mastoid process and the lateral aspect of the anterior part of the frontal.
6) Marked depth of the orbits-The distance from the back of the orbits to the front is large, partly a factor of the large supraorbital torus.
7) Facial prognathism-The maxillas protrude further forward then the exterior part of the orbits.
8) The position of maximum cranial breadth on the supramastoid crests-The cranium is horizontally at its widest near the bottom, usually around where the occipital torus and the top of the mastoid process meet.
9) The superior medial slope of the parietals-This trait produces a unique angle between the parietals. There appears to be three distinct lines that move backwards on the skull, one is at the sagittal suture, the other two are found approximately two thirds down the parietal.
10) The vertical separation of inion and endinion--This trait is inside the skull, thus this feature will not be used due to the inability to see it on the casts and photographs
11) The position of the tympanic crests adjacent to the anterior faces of the mastoid processes-This feature will not be used due to the inability to see it on the casts and photographs.
12) The sagittal and transverse expansion of the nuchal plane-This is the presence of a crest of bone across the occipital just above the nuchal lines where the neck muscles attach.
13) Lack of a vertical edge at the posterior end of the temporal squama-This feature is due to the receding frontal, the temporal/parietal suture is almost horizontally straight, where-as in moderns this suture is much more curved.

Table 1-4 Wolpoff et al (1984)-General Resemblance of Australians to Indonesian

## Hominins

1) Posterior position of the minimum frontal breadth, well behind the orbits-This is also called post-orbital constriction and is due to the frontal narrowing behind the eyes.
2) Flatness of the frontal in the sagittal plane-This is a common trait in all archaic hominins. The frontal is a lot more horizontal in orientation giving the skull a clearly different shape from moderns.
3) The horizontal orientation of the supraorbital's lower border-The lower border between the supraorbital torus and the superior orbit of the eye is horizontal.
4) Distinct prebregmatic eminence-A small point of bone emerging from the joint between the coronal and sagittal sutures, this is part of a frontal/sagittal keel.
5) Marked prognathism-The maxillas protrude further forward then the exterior part of the orbits.
6) The maintenance of large posterior dentitions throughout the Middle and Late Pleistocene-Due to the lack of associated faces with the Ngandong sample, this feature will not be used.
7) The persistence of the Zygomaxillary ridge-The zygomaxillary region is only present on Sangiran 17 and the author cannot see this feature on the cast, therefore this trait will not be used.
8) Eversion of the lower border of the malar-The malar is the combination of the Zygomatic and the maxillary and as stated above the zygomaxillary is only present on Sangiran 17. This feature will not be used because it is only preserved on one specimen and this is not from the temporally late Ngandong series.
9) Rounding of the inferolateral border of the orbits-Once again this feature, the lower orbit being round, is only present on Sangiran 17 and will not be used.

## Specific Resemblances of Australians to Ngandong

10) Well-developed, supraorbital torus discontinuous over glabella but undivided over each orbit-This is a combination of several previously mentioned traits, a supraorbital torus that dips slightly at the midline.
11) A flat, long receding forehead lacking a supratoral sulcus-The frontal is flat and receding and the supraorbital torus leads straight into the frontal.
12) Prelambdoidal depressions-There is the presence of a slight dip at the midline between the parietals immediately before they join the occipital at the lambdoid suture.
13) Sharp angulations between the occipital and nuchal planes-This trait is linked with an occipital torus. The upper part of the occipital is rounded in shape as it leads into the torus, where-as the lower part of the occipital is angled almost horizontal as it move up to the torus.
14) Short sphenoparietal articulations in the pterion regions-This feature will not be used due to the inability to see it on the casts and photographs.

The preceding trait lists were reviewed and many features were either merged or not applied to this test. The author believes that several features should be combined. The supraorbital torus complex should be counted as a single feature. Browridges are present on most hominins at some frequency; it is the specific combination of brow elements that can best represent a regional supraorbital complex. This idea also applies to the occipital torus complex, which should be rated as a single trait. The prelambda depression and raised part on the lambdoidal suture are similar trait observed from opposite viewpoints. For something to be raised, a corresponding point must logically be lower, or depressed. Finally, the presence of a suprameatal tegmen causes the external auditory meacus to be widest in the horizontal plane. Therefore, these items have been merged. Once all the unusable traits and duplications are removed from the list and the newly merged combinations are accounted, the final number of features is eleven. These are reproduced below.

Table 1-5 The Proposed Continuity Traits for Australasia (adapted from Weidenreich, 1949; Larnach and Macintosh, 1974; Thorne and Wolpoff, 1981; Wolpoff et al., 1984)

1) A clear supra-orbital torus, which has a medial sulcus at the glabella. Also, the shelf of bone is orientated more horizontally on its lower border and there is a lack of a sulcus supratoralis behind the browridges.
2) A flat, receding frontal.
3) A prelambda depression, with a corresponding raised occipital at the lambdoidal suture.
4) Strong development of an occipital crest, just above the nuchal line. This crest is the reason for the triangular appearance of the occipital and the distinctions between the upper and lower part of this bone.
5) The presence of a suprameatal tegmen, which makes the external auditory meatus widest in the horizontal plane.
6) The squamous suture is almost horizontal, without a significant arch.
7) Marked post-orbital constriction
8) Facial prognathism
9) The maximum cranial breadth is near the bottom of the skull. The widest point is on the line of the occipital torus to the anterior part of the mastoid process.
10) The angle of the parietals, which slope away from the sagittal suture to a clear angle about two thirds of the way down the bone, then they sharply bending down to meet the temporal bone.
11) The presence of at least a partially sagittal/frontal keel.

## Method and Materials

While the central aim of this thesis is to review purported Australasian lineage contimity, a large amount of work will be devoted to defining and examining Homo erectus, Homo heidelbergensis, Homo neandethalensis and Homo sapiens specimens from all regions where they are discovered. Proving the existence of some purported Australasian characters in modern humans from Australia does not conclusively demonstrate a unique continuity to the exclusion of a modern African origin. However, indicating the lack of these features in other regional hominin populations through time would help establish a large base for MRE. A general overview of this species, with the cramial characteristics that definc it, coupled with dating and history of each specimen will be included. These elements will be discussed in detail. Whenever possible a combination of personnel observations on casts and photographs of the originals were utilized. However, many important specimens were not available as casts. The uses of published photographs did not diminish the reliability of this study, because most of the morphological traits under review are prominent characters on the cranium. Thus, a clear, high-resolution photograph can be used to assess character states. The following specimens will be used in this investigation.

Table 1-6 Hominin Specimens

| Specimen | Species |
| :---: | :---: |
| KNM-ER 3733 | Homo erectus |
| KNM-ER 3883 | Homo erectus |
| KNM-WT 15000 | Homo erectus |
| OH9 | Homo erectus |
| Bou-VP-2/66 'Daka' (p) | Homo erectus |
| Gongwangling (p) | Homo erectus |
| EV 9001 (p) | Homo erectus |
| Sinanthropus reconstruction (Tattersall and Sawyer, 1996) | Homo erectus |
| Sinanthropus reconstruction (Weidenreich, 1937) | Homo erectus |
| Hexian (p) | Homo erectus |
| D2280 (p) | Homo erectus |
| D2282 (p) | Homo erectus |
| Ceprano (p) | Homo erectus |
| Mojokerto (infant) | Homo erectus |
| Sangiran 2 | Homo erectus |
| Sangiran 17 | Homo erectus |
| Trinil 2 | Homo erectus |
| Sambungmacan 3 (p) | Homo erectus |
| Ngandong 1 (p) | Homo erectus |
| Ngandong 5 | Homo erectus |
| Ngandong 6 (p) | Homo erectus |
| Ngandong 9 (p) | Homo erectus |
| Ngandong 10 (p) | Homo erectus |
| Ngandong 11 (p) | Homo erectus |
| Bodo (p) | Homo heidelbergensis |
| Kabwe | Homo heidelbergensis |
| Elandsfontein (Saldanha) | Homo heidelbergensis |
| Lake Ndutu (p) | Homo heidelbergensis |
| Arago 21 (p) | Homo heidelbergensis |
| Petralona (p) | Homo heidelbergensis |
| Atapuerca 4 (Proto-Neanderthal) (p) | Homo heidelbergensis |
| Atapuerca 5 (Proto-Neanderthal) (p) | Homo heidelbergensis |
| Steinheim (Proto-Neanderthal) | Homo heidelbergensis |
| Jinniushan (p) | Homo heidelbergensis |
| Dali (p) | Homo heidelbergensis |
| Maba (p) | Homo heidelbergensis |
| Gibraitar 1 | Homo neanderthalensis |
| Krapina 3 | Homo neanderthalensis |
| La Chapelle-aux-Saints | Homo neanderthalensis |
| Monte Circeo | Homo neanderthalensis |
| Feldhofer 1 | Homo neanderthalensis |
| La Ferrassie | Homo neanderthalensis |

St Cesaire (p)
Tabun 1 (p) Shanidar 1 (p)
Amud 1 (p)
Jebel Ifhoud 1 (p)
LH 18 (p)
Skhul 5
Qafzeh 6 (p)
Qatzeh 9 (p)
Modern African *
Upper Cave 101 (p)
Upper Cave 102 (p)
Upper Cave 103 (p)
Liujiang ( $p$ )
Modern Asian *
Cro-Magnon 1
Predmosti 3
Madec 1 (p)
Wadjak 1
WLH 50 (p)
Lake Mungo 1 (p)
Lake Mungo 3 (p)
Kow Swamp 1 (p)
Kow Swamp 5 (p)
Kow Swamp 7 (p)
Coobool Creek 16 (p)
Coobool Creak 49 (p)
Coobool Creek 65 (p)
Coobool Creek 76 (p)
Cohuna (p)
Keilor (p)
Modern Australian *

Homo neanderthalensis
Homo neanderthalensis
Homo neanderthalensis
Homo neanderthalensis

## Homo sapiens

Homo sapiens
Homo sapiens
Homo sapiens
Homo sapiens
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Homo sapiens
Homo sapiens

Unless noted with a (p) all specimens were reviewed as cast
*-These specimens are produced by Bone Clones

Currently, there is great confusion over the definition of living biological species (see Lambert and Spencer, 1995; Wilson, 1999; Wheeler and Meier, 2000; Wood and Richmond, 2000). Therefore, defining a species from paleontological remains can be tremendously complex. Such fossil taxa must be classed on morphological traits, but
categorization can be subjective (see Lahr 1994 for a quantifiable method of trait identification). Henceforth, the accurate identification and interpretation of features is essential for species identification. A major problem associated with tracking morphological features is trying to decide if they represent the sharing of derived characters, synapomorphies; the sharing of an ancestral condition, symplesiomorphies; the occurrence of derived traits, apomorphies; or are even the result of pathologies, or artificial body modification. For defining a species, apomorphies are preeminent and will be focused on in this work.

The study of the occurrence of Australasian feature is presented in two separate locations, but both utilize similar techniques. The first analysis follows the information concerning the individual species. Each species was independently evaluated against the Australasian continuity traits. This was to observe if there is any pattern, either geographically or temporally, within a single biological group. The second investigation was undertaken once all the data had been assembled and utilizes both qualitative and quantitative inspection. These two evaluations have elucidated information about the origins of modern humans. Both investigations are based on the presence or absence of morphological features on casts and photographs. The creation of an inclusive and total continuity trait list for Australasia allowed for the individual specimens to be scored " 1 " if the feature is present, " 0 " if the feature is absent, or " X " if the feature is not clearly discernable, cannot be described due to missing elements, or an inability to discern the trait on published photographs.

The final analysis used all the species to appraise each modern human origin theory. Each theory has suppositions for the fossil record and can be qualitatively
scrutinized. First, if a complete global replacement occurred, regional lineages could arise until the appearance of modern humans, than these lines should be broken. Modern humans may have some similar features to archaic group because of symplesiomorphic traits and convergent evolution. If convergence occurred, novel apomorphies in modern humans could appear to resemble earlier non-African lineages. Second, with an extreme Multiregional model, lineage continuity should be obvious throughout all successive morphological species originating with Homo erectus. There should be no major break in continuity trait concentration or composition during the transition from archaic and modern human. Finally, in a middle ground hypothesis the transition between archaic and modern humans should involve an alteration in the regional continuity combinations, such that they are still recognizable as particular areas with connections to past regional ancestors, but with a major change in frequency or composition of some features caused by the influx of African DNA.

Comparing and contrasting the presence of the Australasian continuity traits utilizing quantitative methods can further confirm the suggested conclusions from the qualitative analysis. Drawing from a collection of computer programs known as PHYLIP, a discrete character analysis system called 'Mix' was used (Felsenstein, 1993). The 'Mix' freeware program was utilized in this investigation, because it produces quantifiable evidence for this work, although it has been evaluated as being slow. For this study, Wagnar parsimony was utilized. This is because it is unclear if the Australasian traits are truly the ancestral condition. The Wagner parsimony method allows both $0-1$ and 1-0 changes, thus allowing for the reversal of features (Kluge and Farris, 1969). It has been claimed that some features may seem to reappear due to similar
environmental pressures. The use of this method is essential to account for such occurrences. If the fossils of Australian modern humans appear to sort closer to Javan Homo erectus then other Homo sapiens, a degree of continuity appears possible. Whereas, if no particular modern group is closer to Homo erectus, or if modern Africans are the closest, an RAO viewpoint would appear correct.

## Chapter 2--Homo erectus

## Overview

Homo erectus truly marks a milestone in the evolution of humans. This species is the first that we have clear evidence for in the entire Old World. It was the first to reach modern body proportions, with the exception of a brain approximately two-thirds the size of modern humans (Wolpoff, 1999; Tattersall, 2000). They manufactured beautiful Acheulian tools, especially the impressive handaxes. It appears that they emerged through a clear cladogenic event, about 2mya (Rightmire, 1990; Wolpoff, 1999). Multiregionalists would further propose that this was the last true speciation event for the human lineage, everything since then has been a gradual rearrangement of genes (Wolpoff et al., 1984; Wolpoff, 1999).

Representatives of Homo erectus have been found in Africa, China, Europe and the Indonesian island of Java. Eugene Dubois discovered the first specimen of this species in 1891 at the site of Trinil in Java (Shipman 2001). Later, finds were also made at Sangiran and Ngandong. Recently, Thorne and Wolpoff (1981) and Wolpoff et al. (1984) have focused on Sangiran 17 and the Ngandong series as part of the Multiregional hypothesis; while Swisher et al. $(1994,1996,2000)$ have vastly improved our understanding about the chronology of the fossils from this region. The Chinese Homo erectus group was discovered in the late 1920s. Davidson Black worked with the Chinese material from Zhoukoudian for seven years until his death in 1934 (see Sigmon and Cybulski, 1984 for a volume in Black's honor). Franz Weidenreich (1943) reviewed the initial Chinese Homo erectus finds in a significant monograph and it is our debt to
him that the loss of the fossils has not irreparably damaged our ability to discuss this group. Within the last twenty years, several finds in China, especially material from Gongwangling, Yunxian and Hexian, have helped our understanding of Homo erectus. The African representatives of Homo erectus came to light much later, even though this is where the species appears to have originated (Rightmire, 1990). To date African members of Homo erectus have been found at Ternifine (now Tighenif) and Sale in northern Africa, around Lake Turkana, Olduvai Gorge and the middle Awash in eastern Africa and in South Africa, especially at Swartkrans (Rightmire, 1988, 1990; Wood, 1991; Jurmain, 2001; Asfaw, 2002). Finally, within the last couple of years clear evidence of a Homo erectus occupation has been found in Europe, specifically from the former Soviet Republic of Georgia and Italy (Ascenzi, 2000; Clarke, 2000; Gabunia et al., 2000; Jurmain et al. 2001).

It has become common to split Homo erectus into two species (see Andrews, 1984; Stringer, 1984; Groves, 1989b; Wood, 1994; Tattersall and Schwartz, 2000). First, a lineage, known as Homo ergaster, which would inciude many, if not all, of the African finds. Second, an Asian population, which displays several purported derived characters and retains the name Homo erectus. Furthermore, it has been claimed that the African Homo ergaster is itself two distinct species (Tattersall and Schwartz, 2000). It appears to the author that the perceived regional variation could be subsumed into a single species. Rightmire (1996, 1998a, 1998b) asserts that most of the purported apomorphies in the Asian lineage are only variably represented in that population and are found in some of the African specimens. Through careful evaluation, the author discerns that OH 9 and a recent find from Ethiopia, nicknamed 'Daka', obviously display a combination of African
and Asian features (especially Indonesian style brows) and the recent reconstruction of Zhoukoudian Homo erectus by Tattersall and Sawyer (1996) looks similar in many respects to the African KNM-ER 3733 and KNM-WT 15000. Therefore, it appears that the observed difference in morphology is simple variation within a species, the majority probably related to sexual dimorphism. Consequently, in this thesis the name Homo erectus is universally applied to what appear to be a polytypical, but united group.

The latest Homo erectus finds in the West appear just after lmya, but the situation is different in Asia. Homo erectus discoveries from Zhoukoudian establish that this taxa survived until between 500-300kya in China (Rightmire, 1998a; Tattersall and Schwartz, 2001). More interestingly, the Indonesian Homo erectus population appears to have lived for an extended period of time. This is a testament to this regional group of Homo erectus; they survived on the island of Java, relatively unchanged from 1.8 mya to 27 kya (Swisher et al., 1994, 1996). It is not known what led to their eventual extinction, but it is intriguing to note the latest posited date is similar to the time the Neanderthals disappear. Using the Neanderthal situation as a model, it would seem likely that modern humans displaced the Ngandong population, but a possibility of limited gene flow cannot be ruled out. The recognition of the late endurance of the Indonesian population demonstrates that the modern human condition as the single extant member of genus Homo is atypical.

## Traits

The following list of Homo erectus cranial anatomy has been adapted from Rightmire (1988, 1990); Stringer (1984); Wood (1991) and several personal observations. The majority of these features are a mixture of symplesiomorphic and synapomorphic traits. Comparing Homo erectus to the earlier Homo habilis, the symplesiomorphic features include lower facial prognathism, post-orbital constriction, low cranial breadth and an angular torus. The low and long cranial shape, robust bones, extensive browridge development, midline keeling and angled occipital are all synapomorphic features with later hominins. Finally, a brain size average of 1000 c is apomorphic of Homo erectus. The expression of some of these characters does not appear to carry a huge influence, especially keeling of the skull and the development of a large occipital crest. The latter appears related to age and/or sex, whereas, keeling expression varies from extreme to non-existent and seems to be just a variable trait. These characters are scored as either present (1), absent (0), or undetermined (X).

Table 2-1 Homo erectus Cranial Anatomy

1. The crania are long and low, with little to no forehead.
2. An average of 1000 cc brain size, with a range between $700-1250 \mathrm{cc}$. It should be noted that earlier specimens tend to have smaller brains, while later ones have larger cranial capacities.
3. The face and vault are extremely robust
4. Marked lower facial prognathism.
5. Extensive and heavy browridges are aiways present, although there appears to be several distinct types. Additionally, a medial sulcus and sulcus supratoralia are present in some of the specimens. The medial sulcus, when present, is not usually as pronounced as in Homo heidelbergensis and Homo neanderthalensis.
6. The presence of a partial frontal and/or sagittal keel is not uncommon.
7. Severe post-orbital constriction.
8. Occipital planes are usually quite angled, usually with the development of a nuchal torus.
9. The cranium is broadest at the base, usually in line with anterior portion of the mastoid process.
10. The presence of an angular torus on the parietals

Table 2-2 contains all the Homo erectus specimens that will be used in this test. This list compares these fossils to the traits defined above using a presence/absence procedure. There are many more fragmentary remains available, but the author did not believe it would be advantageous to include these specimens. This decision was primarily due to the employment of a trait presence/absence technique, both for the establishment of Homo erectus status and during the exploration of Australasian characters frequency at the end of this chapter. Fragmentary remains would not add a substantial amount of diagnostic characters to the overall sample. Any deviation from the expected morphology will be discussed in the individual descriptions.

Table 2-2 Homo erectus Specimens
Characters \#
Africa
KNM-ER 3773
KNM-ER 3883
KNM-WT 15000
OH9
Bou-VP-2/66 'Daka' (p)
$\begin{array}{lllllllllll}1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & \text { Present Absent }\end{array}$

| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 10 | 0 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1 | 1 | 1 | $X$ | 1 | 0 | 1 | $X$ | 1 | 0 | 6 | 2 |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 9 | 1 |
| 1 | 1 | 1 | $X$ | 1 | $X$ | 1 | 1 | 1 | 1 | 8 | 0 |
| 1 | 1 | 1 | $X$ | 1 | 1 | 1 | 0 | 1 | $X$ | 7 | 1 |

## China

| Gongwangling (p) | 1 | 1 | 1 | $X$ | 1 | $X$ | 1 | $X$ | $X$ | $X$ | 5 | 0 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| EV $9001(p)$ | 1 | $X$ | 1 | 1 | $\times$ | $X$ | $X$ | $X$ | $X$ | $X$ | 3 | 0 |
| Sinanthropus reconstruction | 1 | $X$ | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |
| (Tattersall and Sawyer, 1996) |  |  |  |  |  |  |  |  |  |  |  |  |
| Sinanthropus reconstruction | 1 | $X$ | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |

(Weidenreich, 1937)
Hexian (p)

## Europe

D2280 (p)
D2282 (p)
Ceprano (p)

| 1 | 1 | 1 | $\times$ | 1 | $X$ | 1 | 1 | 1 | $X$ | 7 | 0 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | $X$ | 9 | 0 |
| 1 | 1 | 1 | $X$ | 1 | 0 | 1 | 1 | 1 | 1 | 8 | 1 |

Java

| Mojokerto (Infant) | 1 | 1 | 1 | $x$ | 1 | 1 | 1 | 0 | $X$ | 0 | 6 | 2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sangiran 2 | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |
| Sangiran 17 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 10 | 0 |
| Trinil 2 | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | X | 1 | 8 | 0 |
| Sambungmacan 3 (p) | 1 | 1 | 1 | $X$ | 1 | 1 | 1 | 1 | 1 | $X$ | 8 | 0 |
| Ngandong 1 (p) | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |
| Ngandong 5 | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |
| Ngandong 6 (p) | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |
| Ngandong 9 (p) | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | $X$ | 8 | 0 |
| Ngandong 10 (p) | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | X | 8 | 0 |
| Ngandong 11 (p) | 1 | 1 | 1 | X | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 0 |

Unless noted with a (p) all specimens were reviewed as casts.

## Specimens

There have been two major finds from the East side of Lake Turkana (formerly East Rudolf). The damaged skull KNM-ER 3733 is approximately 1.8 mya, whereas KNM-ER 3883, a calvaria with part of the right face still attached, is slightly younger at approximately 1.6 mya (Rightmire, 1990; Wolpoff, 1999). KNM-ER 3733 clearly meets Homo erectus characteristics; although the nuchal torus is not as developed as in some other specimens. There are extensive cracks present on this find and the occipital is slightly deformed towards the left. KNM-ER 3883 exhibits greater deformation with the left side of the occipital and the left temporal clearly displaced backwards. Furthermore, the cranial base has been pushed up. The combination of these factors has altered the configuration of the occipital and the nuchal planes. This specimen does not exhibit a midline keel on either the frontal bone or along sagittal suture and does not have an angular torus on either of the parietals. Otherwise it meets the criteria of Homo erectus. Both finds have cranial capacities that are rather small, KNM-ER 3733 at approximately 848 cc , while KNM-ER 3883 is slightly smaller at 804cc (Walker and Leakey, 1993).

The remarkably complete Nariokotome boy, designated KNM-WT 15000, was found to the West of Lake Turkana. It is securely dated to 1.5 mya. The cranial capacity has been estimated at 880 cc , which is slightly larger than the earlier finds from East Turkana (Leakey and Walker, 1993). The skull is missing an anterior piece of the frontal, but the beginning of clear browridge appears on the left side. The reconstructed skull is slightly warped. The right side of the occipital and the right temporal bone are noticeably lower than the same elements on the left side. Also, the left parietal is slightly higher than the right. Due to this deformation, the cranial base is shifted towards the right, but
the skull's greatest width is still clearly across the top of the mastoids. The occipital planes are not greatly angled and there is only a faint ridge of bone that could conceivably be a nuchal torus. This individual is a juvenile of approximately 11 years and it is entirely probable that the cranial superstructure would have increased once he reached maturity (Wolpoff, 1999).

A partial cranium, OH 9 , dates between 1.2 to 1.4 mya (Rightmire 1990; Walker and Leakey, 1993; Wolpoff, 1999). Much of the calvaria is missing, including a large part of the frontal, the vast majority of the right parietal, part of the left parietal and a small, anterior piece of the occipital. The specimen is larger than the finds from the Turkana basin, with a brain size of 1067cc (Rightmire, 1990). Apart from an insignificant difference in browridge size and development OH 9 closely resembles Sangiran 17 and several of the Ngandong crania when viewed laterally. This reinforces the idea that Asian and African Homo erectus finds are a single, but polytypic species, with probable sexual dimorphism. Even with the fragmentary nature of this find, it is of importance to this work because it does not appear to have been significantly deformed. Even from the limited elements that are preserved, this specimen meets eight of the ten Homo erectus characters.

While Daka can only be viewed from published photographs, it is indispensable to this investigation due to its temporal location. Asfaw et al. (2002) note that the cranium has been slightly deformed to the left, which can clearly be seen due to the difference in height of the parietals. The cranial capacity of Daka is 995 cc and it is dated to 1.0 mya. In there preliminary analysis of this find Asfaw et al. (2002) state that there is not a true occipital torus, but from published images the author can discern a small ridge
of bone on the occipital. The ridge does not appear to be a true torus, due to the anterior part of the occipital rising vertically, rather than sloping back. This cranium exhibits several interesting character distinct from the typical cranial profile of Homo erectus. First, the anterior of the occipital rising vertically is a character associated with later hominins. Second, Daka and Ceprano, another later Homo erectus found in Europe, exhibit the classic low profile of Homo erectus, but their cranial length is shorter than expected. Until the discovery of further finds from this time period the nature of these alteration cannot be clearly assessed. They could represent presumptive traits of Homo heidelbergensis, or it may be simple chance that the two specimens we currently have from Imya are unusually short skulls, with unique occipital morphology.

Perhaps the most famous Homo erectus material comes from Chinese cave of Zhoukoudian; the so-called Peking man. The story about the loss of the original Zhoukoudian material as they were shipped away from the advancing Japanese army is well known (see Shapiro, 1974). Fortunately, Franz Weidenreich's extensive monograph on these finds allows for their continued contribution to hominin evolution. The Zhoukoudian site is predated by finds from Yunxian and Gonwangling, but it is still the best discovery of Homo erectus from Northern Asia. The site is dated between 550300kya (Tattersall and Schwartz, 2000). The discoveries at Zhoukoudian were quite fragmentary, but several reconstructions have been accomplished. In this thesis two different reconstructions are used: a reproduction of the original recreation made by Weidenreich (1937) and a recently complete reconstruction by Sawyer (Tattersall and Sawyer, 1996). The earlier reconstruction, asserted as female, has several limitations, due to the lack of connections between the elements used and the interpretive nature
employed to produce the midface. The more recent reconstruction utilized larger and more robust cranial fragments and is probably representative of a male (Tattersall and Sawyer, 1996). This reconstruction provides a more complete view of the face of Chinese Homo erectus. Both clearly fit in the classic definition of Homo erectus, with large browridges, an angled occipital with a torus, postorbital constriction and a low, long cranial shape.

The Gongwangling cranial fragments recovered from Lantian, China are believed to be the oldest Homo erectus find in Northern Asia. The specimen is dated between 1.15 mya to 750 kya and has a cranial capacity of 780 cc (Wolpoff, 1999; Brown, 2002). It consists of an incomplete braincase, missing the occipital and the left temporal. There is also a fragment of the right maxilla. These elements are poorly preserved and maybe slightly deformed. Five diagnostic characters are present, which classify Gongwangling with Homo erectus. Unfortunately, four of these features, the shape of the crania, robustness, the presence of a browridge and post-orbital constriction, are symplesiomorphic with the later Homo heidelbergensis. However, Gongwangling does not share any of the derived characters of this later taxa. Due to the lack of later human synapomorphies and its extreme age it best to classify Gongwangling as Homo erectus.

Two badly crushed crania were recovered from Yunxian in China. EV 9002 is crushed flat and distorted towards the right; due to these limitations it will not be used in this study. EV 9001 cranium is also badly deformed and only three characters from table 2-1 could reliably be used to establish this find as Homo erectus. All the preserved features can be symplesiomorphic with later archaic hominins, but due to a mean age estimate of 581 kya these finds seems best assigned to Homo erectus (Brown, 2002; but
compare to Wolpoff, 1999). The age recorded for these crania is after the appearance of Homo heidelbergensis in African and Europe, but before the disappearance of Homo erectus in China. Furthermore, the first clear Chinese representative of Homo heidelbergensis does not occur until around 300kya. Despite the temporal information, Rightmire (1998a) has described several possible derived characters in EV 9001 that are synapomorphic of later hominids, including a relatively large brain case, only minor postorbital constriction and an arched squamous suture. The large brain is not remarkable when compared to some of the later finds from Zhoukoudian and Ngandong in Java. From published photographs, it appears that the browridges of EV 9001 are extremely damaged; therefore the amount of post-orbital constriction could be underestimated. The major abnormality is the arched squamous suture. Unless more complete finds from this time period are discovered, the significance of this derived suture configuration on EV 9001 cannot be evaluated. It could represent early evidence of contact between AfroEuropean Homo heidelbergensis and Chinese Homo heidelbergensis, the appearance of a more advanced Chinese form separate from the Afro-European Homo heidelbergensis, or it may just be an unknown part of normal Homo erectus variation. If the latter is the case, then the synapomorphic trait of an arched squamousal shape that is used to define Homo heidelbergensis needs to be reviewed.

Homo erectus discoveries from Hexian County are contemporaneous with, or maybe slightly younger than the finds from the Zhoukoudian lower cave (Brown, 2002). For this investigation the Hexian skullcap has been included as a representative of Homo erectus, but this assignment is problematic. This specimen has a long, low profile and browridges like Homo erectus, but the frontal bone is expanded, the parietals appear quite
broad and the squamous suture is arched, which is like later hominins. Wolpoff (1999) links the expanded frontal to the later Dali cranium. While Brown (2002) asserts that the parietals are broad because they have been pushed down and are deformed. If Asian Homo heidelbergensis specimens are an in situ development, this specimen could be classed as intermediary between Homo erectus and the more advanced Chinese hominins.

Work at the Dmanisi site in the former Soviet Republic of Georgia produced a damaged mandible, a calvaria and a relatively complete cranium with some damage to the mid-face area (Jurmain et al., 2001; Gabunia et al., 2000). The mandible is missing the ascending ramus from both sides, but has all the teeth preserved. Its inclusion into Homo erectus is based on its lack of chin and an extremely early date of 1.8 to 1.6 mya (Jurmain et al., 2001). The assertion that this site was home to Homo erectus was confirmed by the discovery of a relatively complete calvaria, designated D2280, and a cranium, known as D2282. Both specimens meet the designated Homo erectus characters in table 2-1. However, both specimens have quite small cranial capacities, 780cc for D2280 and an estimated 650cc for D2282 (Gabunia et al. 2000).

The much later Ceprano calvaria was discovered in Italy in 1994. The specimen dates between $800-900 \mathrm{kya}$ and is currently the extreme Northeastern boundary for Homo erectus in Europe. It has twice been reconstructed due to its fragmentary nature, caused by a bulldozer. In addition, post-mortem deformation; observed in a superior view the right side of the occipital and right parietal are clearly pushed inward. The current reconstruction was accomplished by Clarke (2000), with some minor modification covered in Ascenzi et al. (2000). The robust skull is clearly Homo erectus, with welldeveloped browridges, an angled occipital and an estimated cranial capacity of 1057 cc .

Ascenzi et al. (2000) note, though, a few morphological distinctions that do not align this specimen with most Homo erectus skulls, mainly the cranium's short length and its lack of post-orbital constriction relative to the expected average. Finally, this specimen does not have a sagittal or frontal keel, but this trait may be variable in Homo erectus.

The Mojokerto infant is a damaged calvaria, but is very important because of its extreme age. Swisher et al. $(1996,2000)$ advanced a date of 1.81 mya, which is close to the earliest known age for African Homo erectus. In a recent review, Anton (1997) narrowed the developmental age range of this individual to between 4-6 years. Large portions of the frontal, parietals and the occipital are preserved, although none of these elements are complete. Some of the general characteristics of Homo srectus are preserved, but there are several problematic features that blur this taxonomic contention. These include the small amount of the brow that is preserved and the developmental age of the individual. While only a fragment of the browridge is preserved on the left side, it clearly projects forward and to the left. This fragment also suggests that the individual had post-orbital constriction. The developmental age range that was established by Anton (1997) indicates that the cranial superstructures have yet to fully develop, which explains the lack of a nuchal torus and a well-defined angular torus.

The Sangiran 2 calvaria was recovered in 1937 and dates to about 1.2mya (Rightmire 1990; Wolpoff, 1999). While the skullcap preservation is acceptable, much of the calvaria has been reconstructed from many small fragments. The browridge is missing entirely from the right side and only a segment remains on the left. From this brow fragment it is clear this individual had post-orbital constriction on the left side.

Generally, this specimen exhibits all of the Homo erectus characters, except lower facial prognathism; which is not surprising as the face is not preserved on this find.

Sangiran 17 is an extremely important find, because it is the only published Indonesian Homo erectus with the facial bones preserved. The find has been dated between 1.2 mya to 700 kya (Stringer, 1996; Wolpoff, 1999). Unfortunately, the frontal, parietals and occipital are extremely fragmentary and several large parts of the braincase are missing. Even with this problem, the browridges, the frontal slope and the shape of the occipital are all clearly similar to Trinil 2 and Sangiran 2. The current reconstruction of the face appears to be to squashed in the vertical axis. This deficiency has been noted by other authors who have commented on the extremely small size of the nasal c pening (Rightmire, 1990, Tattersall and Schwartz, 2000).

The earliest discovery of Indonesian Homo erectus occurred in October 1891 at the site of Trinil. Eugene Dubois found several fragmentary elements including a skullcap known as Trinil 2 (Shipman, 2001). This specimen has been dated to between 700kya to 1.2 mya (Wolpoff, 1999; Tattersall and Schwartz, 2001). It is missing its face and the lower parts of the cranium, including both temporal bones and a large part of the occipital. Additionally, the browridge is damaged and worn down, although the preserved left third clearly demonstrates this individual had a large orbital torus and postorbital constriction. Finally, it is possible that Dubois partly reconstructed the posterior parts of the parietals (Rightmire, 1990). The preserved parts place this specimen unmistakably in Homo erectus.

Two crania and a tibial fragment have been recovered from the Sambungmacan District in Indonesia. They have been dated to between 300-100kya (Laitman and

Tattersall, 2001; Marquez et al, 2001). For this investigation, only Sambungmacan 3 will be used, because it received detailed treatment when it was discovered in New York City (see Broadfield et al., 2001; Delson et al., 2001; Marquez et al., 2001). This specimen is clearly Homo erectus, but has several unusual features. First, the frontal rises quite sharply when compared to other Homo erectus finds. Second, the cranial vault is more globular in shape, thus it appears slightly more modern (Marquez et al., 2001). The Sambungmacan 3 cranium is missing part of its cranial base and the entire face, but otherwise the specimen is complete. It has clear post-orbital constriction, a small occipital crest and the browridges that are quite reduced over the nose.

There have been 11 crania and 2 tibia recovered from the Ngandong site on the Solo river in Java (Weidenreich, 1951). It is believed that crania 1, 4, 6 and 8 are female, while $2,5,9,10$ and 11 are male, with Ngandong 2 being a juvenile. The average cranial capacity from this site is 1135 cc . Several of the specimens exhibit a large reduction in the medial portion of the browridge (Wolpoff, 1999). A recent re-dating of this site has proved controversial. Swisher et al. (1996) have proposed a date range between 27 to 53 kya . It was previously believed that these fossils were much older, and Wolpoff (1999) still posits a date of 250 kya with a margin of 200,000 years on either side. For this thesis, Ngandong $1,5,6,9,10$ and 11 were utilized, due to their relative state of completion. Ngandong 1 is a partial calvarium missing the left temporal, much of the cranial base and parts of the left browridge. Ngandong 5 is a slightly more complete skullcap, with both temporal bones present, but the cranial base is not preserved. Calvarium 6 is almost complete, only missing a third of the left browridge. Ngandong 9 is a fragmentary skullcap that is $s$ missing parts of both parietals and the entire cranial
base. There is also slight damage to the right browridge. Specimen number 10 is another relatively complete calvarium with damage to the left browridge and no preserved cranial base. This find does not have the standard flat browridge that is common to the Ngandong hominins and is a purported Australasian trait. The orbital torus curves down at a quite sharp angle approximately half way along the right browridge. Finally, Ngandong 11 is the most complete calvarium, with an intact cranial base and browridges. This specimen is only missing a portion of the left mastoid process.

Table 2-3 Australasian Features in Homo erectus

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Austraasian Characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | Present | Absent |  |
| Africa |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| KNM-ER 3733 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 7 | 4 |
| KNM-ER 3883 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 7 |
| KNM-WT 15000 | 1 | 1 | $X$ | 1 | 0 | $X$ | 1 | $X$ | 1 | 1 | $X$ | 7 | 6 | 4 |
| OH9 | 0 | 1 | $X$ | 0 | $X$ | $X$ | 1 | $X$ | 1 | $X$ | 1 | 4 | 2 |  |
| Bou-VP-2/66 'Daka' (p) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

China
Gongwangling (p)
EV 9001 (p)

| 0 | 1 | $X$ | $X$ | $X$ | $X$ | 1 | $X$ | $X$ | $X$ | $X$ | 2 | 1 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $X$ | 1 | $X$ | $X$ | $X$ | 0 | $X$ | 1 | $X$ | $X$ | $X$ | 2 | 1 |
| 0 | 1 | 0 | 1 | 0 | $X$ | 1 | 1 | 1 | 1 | 1 | 7 |  |

Sinanthropus reconstruction
(Tattersall and Sawyer, 1996)
Sinantropus reconstruction
(Weidenreich, 1937)
Hexian (p)
Europe
D2280 (p)
D2282 (p)
Ceprano (p)

| 0 | 1 | $X$ | 1 | 1 | $X$ | 1 | $X$ | 1 | $X$ | $X$ | 5 | 1 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1 | 1 | $X$ | 1 | 1 | $X$ | 1 | 1 | 1 | $X$ | 1 | 8 | 0 |
| 0 | 1 | $X$ | 1 | $X$ | $X$ | 1 | $X$ | 1 | 1 | 0 | 5 | 2 |

Java

| Moiokerto (infant) | X | 1 | X | 0 | X | X | 1 | $x$ | $x$ | 0 | 1 | 3 | 2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Mojokerto (infant) | X | 1 | 0 | 1 | 1 | 1 | 1 | X | 1 | 1 | 1 | 8 | 1 |
| Sangiran 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 10 | 1 |
| Trinil 2 | X | 1 | X | 1 | X | X | 1 | X | X | 1 | 1 | 5 | 0 |
| Sambungmacan 3 (p) | 1 | 1 | X | 1 | X | 1 | 1 | X | 1 | X |  | 7 | 0 |
| Ngandong 1 (p) | 1 | 1 | X | 1 | 1 | X | 1 | X | 1 | 1 |  | 10 | 0 |
| Ngandong 5 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | X | X 1 | 1 |  | 10 | 0 |
| Ngandiong 6 (p) | 1 | 1 | X | 1 | 1 | X | 1 | X | 1 | 1 |  | 8 | 0 |
| Ngandong 9 (p) | 1 | 1 | X | 1 | 1 | X |  | X | 1 | 1 |  | 7 | 1 |
| Ngandong 10 (p) | 0 | 1 | X | 1 | 1 | X |  | X | 1 | 1 |  | 8 | 0 |
| Ngandong 11 (p) |  | 1 | X | 1 | 1 | X |  | X |  | 1 |  | 8 | 0 |

Unless noted with a ( $p$ ) all specimens were reviewed as casts.

In relation to the presence of Australasian traits it is immediately clear that there is a small favoring of Indonesian Homo erectus. Overall the Java specimens have a lower frequency of absent features; usually 1 to 0 . It may appear that the mainland Asian finds also have few absent features, but due to their limited and fragmentary nature this may not be accurate. The recent Zhoukoudian reconstruction demonstrates that a relatively complete Chinese fossil has three absences. This seems to fit in the regular variation found in the African and European samples. Sangiran 17 and Ngandong 5 have the greatest frequency of regional traits, each displaying 10 out of the 11 . The other remains from Ngandong also have many of the regional features, but due to the state of preservation, or quality of the photographs none of them display the full suite. However, this slight alignment with Java does not conclusively prove the MRE viewpoint. There are two major problems that work against this position: the presence of every Australasian trait in fossils from other regions and the late date for the Ngandong fossils.

Each of the suggested Australasian features is found in every other region. However, MRE has claimed that it is a unique combination of these features represents this Australasia (Wolpoff et al., 1984). For the earliest hominin ancestor that traveled beyond Africa there does appear to be such a combination. The difference between the Indonesian and other Homo erectus specimens is slight, but it could be argued that this is the beginning of a lineage with these traits. The major problem with this argument revolves around when these features disappear from other regions. Homo erectus may have lived in Java for 250 kya longer then in any other regions, thus preserving these features. However, do the new hominin species in Africa, Europe and China display the Australasian traits? Or does the combination of these features reduce in these other
areas? These questions will be addressed through the following several chapters that examine the next three species of hominins.

One further element should be noted, the age of the hominins from Ngandong. The recent redating of the Ngandong fossils to 27 to 53 kya has major implications for this study (Swisher et al., 1994). While each of the specimens used in this analysis are clearly Homo erectus, the African and European material is much earlier than Ngandong. Homo heidelbergensis and the later Homo neanderthalensis and Homo sapiens had already replaced Homo erectus in both of these regions. Additionally, the comparatively late EV 9001 and Hexian finds from China may have to be excluded from this species due to their appearance of anticipating the Chinese Homo heidelberginsis condition. Therefore, Ngandong is not similar to the hominins that exist in other regions during the same time, rather they represent the last bastions of the Homo erectus condition.

While the above date may not agree with a strong MRE model, it does still allow for potential interbreeding between this late Homo erectus group and other hominins. The traits proposed as Australasian features are clearly present within all Homo erectus populations and it would seem that there continuation into any group of modern humans would have to be due to either primitive retention of these archaic features or interbreeding. Except for one unusual modern European, Predmosti 3, these archaic characters are lost in other regions by 50 kya , whilst they are still present on the island of Java. The late date of Ngandong is crucial to understanding from which population these traits could be retained.

## Chapter 3-Homo heidelbergensis

## Overview

The sample of hominins from the Middle Pleistocene, about 730kya to 130kya, provides a complex picture into the evolution of several unique human lineages (Stringer, 1985). Some of the most important changes in the human organism occurred during this time, including a large increase in cranial capacity and the foundation for the skull form that is the hallmark of Homo sapiens (Rightmire, 1998a). This time of human evolution was underrepresented for many years. Before the 1930s, the best-known and most complete fossils from this period were from Asia, but these are representatives of Homo erectus. The only major find in the West was from Germany. This discovery dates to about 400 kya and consists of an extremely robust mandible from a site near the village of Mauer, which is close to Heidelberg (Howell, 1960; Wood and Richmond, 2000). Schoetensack (1908) described this find as the type specimen for Homo heidelbergensis. Both Howell (1960) and Rightmire (1996) note that this specimen is not like Homo erectus, but it is more primitive than modern jaws. This description of an intermediate morphology with both archaic and derived traits corresponds to the general portrayal of Homo heidelbergensis.

Beginning in the 1930s important finds began to remedy the gap in knowledge about Middle Pleistocene fossils in Europe. The discovery of the Steinheim cranium, which dates to between $300-200 \mathrm{kya}$, clearly establish a long history of occupation in Europe (Howell, 1960; Wood and Richmond, 2000). This specimen has a clear link to the later Neanderthals including a double arched browridge and mid-facial prognathism, but in profile it appears similar to the Petralona skull. Finds from Petralona, Greece in

1959 and Arago, France in the late 1960s helped refine knowledge of earlier Middle Pleistocene Europe hominins. Both of these specimens have possible presumptive Neanderthal traits, but are clearly linked to African representatives of Homo heidelbergensis (Rightmire, 1988, 1996, 1998a; Wood and Richmond, 2000). In the last several decades, sites from the Sierra de Atapuerca in Spain have further enhanced our understanding of Homo heidelbergensis. The Sima de los Huesos location has elucidated how the European branch of Homo heidelbergensis is related to the Neanderthals. For example, cranium 4 displays clear mid-facial prognathism (Arsuaga et al., 1997). At the same time, the Gran Dolina site, dated to 780kya, has raised the possibility of an earlier taxa from Europe known as Homo antecessor (Arsuaga et al., 1999). Unfortunately, due to the fragmentary nature of the specimens from the latter location, they cannot be included in this study.

A number of excellent finds from Africa have added to our understanding of Homo heidelbergensis. In 1921 a cranium from the Broken Hill mine, near Kabwe, was named as Homo rhodesiensis. This Zambian skull is especially similar to the Petralona cranium and the Arago 21 partial face (Rightmire, 1988, 1998a). A skullcap with a similar shape to Kabwe was found in 1953 in Elandsfontein, South Africa (Wood and Richmond, 2000). The 400kya Lake Ndutu partial cranium from Tanzania is possibly a female representative of Homo heidelbergensis (Rightmire, 1990; Wolpoff, 1999). Finally, a partial cranium from Ethiopia, known as Bodo, is the earliest example of Homo heidelbergensis and is dated to 600 kya (Rightmire, 1996).
G. Phillip Rightmire (1988, 1990, 1996, 1998a) has been a vocal influence in the establishment of Homo heidelbergensis as a true species. Previously, African and

European specimens from the Middle Pleistocene have been allocated to several grades of 'archaic' Homo sapiens (Brauer, 1984, 1989; Stringer, 1985). The term 'archaic' Homo sapiens has been recognized as unacceptable and the system of classification utilizing grades to distinguish morphological differences between points in a lineage has been altered to reflect the more punctuated nature of evolution (Stringer 1992b; Tattersall, 2000). Currently, many biological anthropologists view morphological distinctions between members of a lineage as a valid reason to separate groups into distinct evolutionary units, or species (Rightmire 1988; Tattersall and Schwartz, 1998; Tattersall, 2000).

As presently defined, Homo heidelbergensis includes specimens from Europe and Africa, but there are also fossils from Asia that display an intermediate morphology between Homo erectus and later hominins. Several specimens from China including Dali, Maba and Jinniushan could be added to Homo heidelbergensis. These fossils have modern features including increased parietal expansion causing a rounder skull and reduction of the occipital crest, but they also preserve large browridges, low vaults and flat foreheads (Etler, 1996). According to Rightmire (1998a), there appears to be either an in-situ evolution from Chinese Homo erectus to a more modern form, or an influx from an Afro-European Homo heidelbergensis. For the supporters of the former, this group has been traditionally termed as pre-modern Homo sapiens, but this name probably should be subsumed by a true species designation. It has been suggested that most Asian hominins display several unique Mongoloid features, including shovel-shaped incisors, mid-sagittal keeling, metopic sutures and flat faces (Wolpoff, 1999). The presence of these features in pre-modern Homo sapiens could discount an exclusive Afro-European
origin (Etler, 1996). The overall construction of Chinese Homo heidelbergensis is similar to the eastern group of Homo heidelbergensis, although the morphology of the face is less prognathic and appears more modern. While these problems need to be answered, for this thesis it is assumed that the Asian specimens are part of a diverse taxon, rather then a unique species.

## Traits

The following cranial feature information has been adapted from Rightmire (1988, 1996); Stringer (1985); and some personal observations. Homo heidelbergensis is a unique combination of archaic and modern features, there only appears to be two apomorphic features. The unique traits are the shape of the browridge, which are thick medially, but taper laterally, and the brainsize. The expansion of the brain is a shared characteristic of all recent hominin species, but the actual cranial capacity does seem to be unique to Homo heidelbergensis. The general robustness of the vault and the low frontal are symplesimorphic with Homo erectus. Finally, the rounding of the skull, shape of the squamous suture and a more vertical occipital bone are synapomorphic with Homo sapiens and Homo neanderthalensis. These characters are scored as either present (1), absent (0), or undetermined (X).

## Table 3-1 Homo heidelbergensis Cranial Anatomy

1. Relative rounding of the skull, due to increased frontal length and parietal width.
2. Dramatically increased brain size relative to Homo erectus-around 1300 cc .
3. Browridges taper as they move laterally from the midpoint, tend to have a medial sulcus.
4. Squamous suture is arched like in moderns.
5. The upper part of the occipital is more vertical as it moves towards the nuchal crest area.
6. Skull is still extremely robust, with thick vault bones
7. Flat, receding frontal

Table 3-2 contains all the Homo heidelbergensis specimens that will be used in this test. This list compares these fossils to the traits defined above using a presence/absence procedure. There are some fragmentary remains available, but these
were excluded from the current study due to their incomplete state. This decision was primarily due to the employment of a trait presence/absence technique, both for the establishment of Homo heidelbergensis status and during the exploration for Australasian characters frequency at the end of this chapter. Fragmentary remains would not add a substantial amount of diagnostic characters to the overall sample. Any deviation from the expected morphology will be discussed in the individual descriptions.

Table 3-2 Homo heidelbergensis Specimens

| Character\# | 1 | 2 | 3 | 4 | 5 | 6 | 7 | Present | Absent |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Africa |  |  |  |  |  |  |  |  |  |
| Bodo (p) | 1 | 1(1300cc) | 1 | 1 | X | 1 | 1 | 6 | 0 |
| Lake Ndutu (p) | 1 | $0(1100 \mathrm{cc})$ | X | X | 1 | 1 | 1 | 4 | 1 |
| Elandsfontein (Saldanha) | 1 | 1(1250cc) | 1 | X | X | 1 | 1 | 5 | 0 |
| Kabwe | 1 | 1(1280cc) | 1 | 1 | 1 | 1 | 1 | 7 | 0 |
| Europe |  |  |  |  |  |  |  |  |  |
| Arago 21 | X | X | 1 | X | X | 1 | 1 | 3 | 0 |
| Petralona (p) | 1 | 1(1230cc) | 1 | 1 | 1 | 1 | 1 | 7 | 0 |
| Atapuerca 4 (Proto-Neanderthal) | 1 | 1(1390cc) | 1 | 1 | 1 | 1 | 1 | 7 | 0 |
| Atapuerca 5 (Proto-Neanderthal) | 1 | $0(1125 \mathrm{cc})$ | 0 | 1 | 1 | 1 | 1 | 5 | 2 |
| Steinheim (Proto-Neanderthal) | X | $0(1100 \mathrm{cc}$ ) | 0 | 1 | 1 | 1 | 1 | 4 | 1 |
| China |  |  |  |  |  |  |  |  |  |
| Dali (p) | 1 | O(1120cc) | 0 | 1 | 1 | 1 | 1 | 5 | 2 |
| Jinniushan (p) | 1 | 1(1260cc) | 0 | + | 1 | 0 | 1 | 5 | 2 |
| Maba (p) | 1 | X | 0 | X | X | X | 1 | 2 | 1 |
| Unless noted with a (p) all spec | i | ere review |  |  |  |  |  |  |  |

## Specimens

The partial male cranium from Ethiopia known as Bodo is of supreme importance because its age and morphology imply that it lies close to the speciation event from Homo erectus. The cranium consists of most of the frontal, parts of both parietals and the left temporal, but the occipital is not present. The fossil is dated by faunal analysis to about 600 kya (Rightmire, 1996). This find appears more robust than later Homo heidelbergensis specimens and displays moderate post-orbital constriction, a frontal/sagital keel, a low profile and a clear angular torus on the parietals. It also appears to retain a very prognathic face similar to Homo erectus. The cranium displays several advanced features including a large brain of approximately 1250 cc , a longer frontal and the maximum cranial breadth appears to be higher then the top of the mastoid process (Rightmire, 1996; Conroy et al., 2000).

The female Homo heidelbergensis find from Lake Ndutu in Tanzania is a partial cranium that is quite weathered. The dating of this specimen is not entirely certain, but if an associated tuft is the same as the upper part of the Masek beds of Olduvai the cranium is about 400 kya (Rightmire, 1990). The specimen consists of parts of the face, the anterior part of the frontal, parts of the parietals and temporals and a complete occipital. The archaic features present include thick vault bones, moderate post-orbital constriction and a brain size of 1100 cc ; although this last feature may be due to sexual dimorphism. The modern features include parietal bossing, a vertical upper occipital and no keel or angular torus. It should be noted that the frontal looks steep, but this is due to the reconstruction (Rightmire, 1998a, 1990).

The Elandsfontein (Saldanha) skullcap from South Africa had initially been identified as a member of Homo rhodesiensis (Day, 1977). Therefore, as Kabwe is now part of Homo heidelbergensis this specimen can also be included in this species (see Rightmire, 1998). The cranial capacity is approximately $1200-1250 \mathrm{cc}$. The age is not known, but a late Middle Pleistocene date has been suggested (Day, 1977). This find clearly has the cranial shape and browridge morphology of Homo heidelbergensis. It is missing parts of both parietals, the posterior part of the occipital and piece of both browridges.

The Kabwe (formerly Broken Hill) cranium from Zambia is an extremely important find. It was placed in its own species, Homo rhodesiensis, but can be subsumed into Homo heidelbergensis. According to Larsen et al (1998), this male specimen has been dated by faunal association to approximately 125 kya , but other authors posit an earlier date around 700-350kya (Rightmire, 1998; Wolpoff, 1999). It displays a mixture of primitive and derived traits that place it between Homo erectus and more modern humans. The cranium displays all five derived traits of Homo heidelbergensis, coupled with a low profile and robust features. The skull profile, while still low, appears to be more curved when compared to Homo erectus, due to increased parietal size. The brain size is large at 1280cc (Wolpoff, 1999). The browridges, while still very large, are reduced in size at the lateral edges. The upper element of the occipital is expanded and more vertical, while the occipital torus is smaller than found on an average Homo erectus. Overall, the robust elements of the cranium are reduced. It is still slightly prognathic, with marked post-orbital constriction, a small angular torus and a frontal keel. Furthermore, the maximum cranium breadth is still across the anterior part
of the mastoid processes. Several other finds were made at the Kabwe site, including post-cranial remains, but these cannot be directly associated with the cranium (Rightmire, 1990).

The French Arago 21 specimen is a reconstructed face, including much of the frontal, maxilla and zyogmatic arches. There have been problems dating this specimen, but a recent synthesis of ESR, fission track, TL, paleomagnetic and U series dates indicates that it is approximately 450 kya (Schwartz and Tattersall, 2002). While the face of this female is robust with thick browridges, it displays modern features including a broad frontal, with lessened post-orbital constriction and the lack of a frontal keel. Additionally, Araso 47 displays parietal bossing (Rightmire, 1990; Wolpoff, 1999). There are also several presumptive apomorphic traits of Homo neanderthalensis present in Arago 21, including slightly more arched browridges and mid-facial prognathism (Arsuaga et al., 1997).

The Petralona cranium, found in Greece, is missing only the right zygomatic arch, parts of the cranial base and some of the interior elements of the nasal cavity. The dating of this find had been challenging, but recent work by Grun (1996) has established a range between 250-150kya. This male specimen is similar to both Bodo and Kabwe and has a broad frontal, with lessened post-orbital constriction, large browridges, a sagital keel, a moderate angular torus and a vertical anterior piece of the occipital (Rightmire, 1990; Wolpoff, 1999). It is also comparable to Kabwe and possibly Homo erectus due to a high degree of pneumatization (Seidler et al., 1997). Therefore, the find displays a combination of archaic and derived traits. According to Wolpoff (1999), the zygomatic morphology foreshadows the Neanderthal condition.

The Sierra de Atapuerca in Spain has been a major location for Middle Pleistocene hominin fossils. As previously discussed, the Gran Dolina site cannot be used due to the fragmentary nature of the finds (see Arsuaga et al., 1999 for information about these partial remains). The later finds from the Sima de los Huesos provide two specimens that can be reviewed. Atapuerca 4 and 5 were dated by $U$ series and ESR to a minimum of 200 kya and are probably less then 300 kya . This date is compatible with the faunal information found at the site (Arsuaga et al., 1997). Atapuerca 4 is a virtually complete male calvarium, lacking a small part of the glabellar region. The specimen bas every trait that characterizes Homo heidelbergensis, including a cranial capacity of about 1390 cc and browridges that thin laterally. It does not appear to display the features used to classify the Neanderthals in table 4-1 and it has several archaic traits, including a frontal keel and angular torus, that are lost in Homo neanderthalensis. On the other hand, Atapuerca 5 appears to display several presumptive Neanderthal traits of the face. This specimen is a complete adult cranium and is either a small male, or a female. The brain size, 1125 cc , is smaller than expected for Homo heidelbergensis. If this specimen were female, it would help to redefine the characters for Homo heidelbergensis, because the other female specimen, Lake Ndutu, also has a brain size under the limit imposed for this species. The face is large relative to the braincase, has noticeable mid-facial prognathism and a large retro-molar space, which are all traits found in Neanderthals. However, it does have a weak angular torus and a keel on the anterior part of frontal (Arsuaga et al., 1997). Additionally, the browridges do not narrow as they move laterally, as is seen in Homo heidelbergensis, but they are not shaped like later Neanderthal browridges (Arsuaga et al., 1997; Wolpoff, 1999). Atapuerca 5 is the most complete European

Middle Pleistocene specimen yet found and its connections to Homo neanderthalensis cannot be denied, but even with these presumptive Neanderthal traits it still appears to fit in Homo heidelbergensis.

The Steinheim cranium from Germany appears to be intermediate between Homo heidelbergensis and the Neanderthals. This specimen has been dated to between 300 200kya (Wood and Richmond, 2000). The decision to include it with the former species is due to a combination of age and similarity to Petralona. Viewed laterally both the Steinheim and Petralona cranial shape appear analogous. There are several features that appear to align the find with the Neanderthals, including a double browridge, mid-facial prognathism and the presence of suveral unique nasal apomorphies (Schwartz and Tattersall, 1996). However, Wolpoff (1999) has claimed that some of these features are not the same as those that appear in Homo neanderthalensis. A further problem is the preservation of this specimen. While all of the cranial bones are preserved, except for part of the base, they appear to have been deformed. An additional predicament concerns the small cranial capacity of the specimen, which is between 900 cc to 1100 cc (Wolpoff, 1999; Schwartz and Tattersall, 2002).

Dali, found in the 1980s, is an almost complete Chinese cranium (Etler, 1996). It has been dated to 209 kya and has a cranial capacity of 1120 cc (Larsen et al., 1998). The specimen does appear to have been slightly deformed; the maxilla has been pushed upwards. It has quite large browridges that thin over the nasal region. The orbital torus of this specimen appears slightly more rounded then is common for Homo heidelbergensis. There are several advanced traits, including a relatively high cranial breadth, an enlarged frontal and parietal bossing. There are also several archaic features,
including a sagittal keel and an angular torus (Wolpoff, 1999). Overall, the specimen appears to display a combination of features very similar to the Afro-European Homo heidelbergensis fossils. Wolpoff (1999) did note several features that may link Dali with Zhoukoudian Homo erectus and later Asian population. This includes flatness of the face, which distinguishes Dali from western specimens.

The Jinniushan find included a cranium and a partial skeleton of a female. The find has an ESR date of 165-195kya and a cranial capacity of 1260cc (Etler, 1996; Wolpoff, 1999). This find presents a combination of modern and archaic features similar to other Homo heidelbergensis specimens. The vault has thin bones, a broad frontal and a relatively gracile occipital, but also displays a large browridges and an occipital torus. The browridges thin over the nose, which is similar to Dali. Wolpoff (1999) believes that this find is similar to the earlier Zhoukoudian Homo erectus.

The final contender of Homo heidelbergensis from China is the Maba cranial fragment (Etler, 1996). This find consists of a partial upper face and a small amount of the parietals. The occipital, lower face and cranial base are not present. The specimen preserves a browridge that seems similar in morphology to Dali and Jinniushan. Wolpoff (1999) has stated that this fragment is similar to other East Asians.

## Australasian Comparison

## Table 3-3 Australasian Features in Homo heidelbergensis

| Australasian Characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |  | es | Absent |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Africa |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Bodo (p) | 0 | 1 | X | X | X | X | 1 | 1 | X | 1 | 1 | 5 | 1 |
| Kabwe | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 7 | 4 |
| Elandsfontein (Saldanha) | 0 | 1 | 0 | 1 | X | X | 1 | X | X | 0 | 0 | 3 | 4 |
| Lake Ndutu (p) | X | 1 | X | 1 | X | X | X | 1 | X | 0 | 0 | 3 | 2 |

## Europe

| Arago 21 (p) | 0 |  | X |  | x | X | 1 | $1$ | x |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Petralona (p) | 0 | 1 | X | 0 |  |  |  |  | 1 | x | 0 | 4 |  |
| Atapuerca 4 (Proto-Neanderthal) (p) | X | 1 | X | 0 |  |  | X |  |  |  |  | $1$ |  |
| Atapuerca 5 (Proto-Neanderthal) (p) | 0 | 1 | 0 | 1 |  | - | 1 | 1 | X |  |  | 6 |  |
| Steinheim (Proto-Neanderthal) |  |  | 0 |  |  |  |  |  |  |  |  |  |  |

## China

| Jinniushan (p) | 0 | 1 | $X$ | 0 | $X$ | 0 | 1 | 0 | $X$ | $X$ | $X$ | 2 | 4 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Dali (p) | 0 | 1 | $X$ | 0 | 1 | 0 | $X$ | 0 | 0 | 0 | 0 | 2 | 7 |
| Maba (p) | 0 | 1 | $X$ | $X$ | $X$ | $X$ | 1 | $X$ | $X$ | $X$ | $X$ | 2 | 1 |

Unless noted with a (p) all specimens were reviewed as casts.

Homo heidelbergensis is an important step in hominin evolution, due to the appearance of features found in modern humans. Many of the changes towards modernity also alter the presence of Australasian regional traits. In Homo erectus the Australasian traits were found in all regional populations, but by the Middle Pleistocene this has changed. No known Homo heidelbergensis has a flat squamosal suture, or the orbital torus shape found in the Ngandong series. All regional populations still display flat frontals and post-orbital constriction, which are clearly symplesiomorphic retentions from Homo erectus. Further shared ancestral traits are found in the European and

African specimens, including prognathic faces and variable occurrences of occipital crests, angular tori and midline keeling. None of these traits are present on Dali, which is the only Chinese specimen that can be reviewed at great length. Furthermore, only the Dali cranium has a horizontal external auditory meatus. There are several important things that emerge from the assessment of this species, including the difference between western and eastern representatives of Homo heidelbergensis and the rapid reduction in Australasian features.

One of the surprising results that emerged from this investigation is the difference between the Chinese and Afro-European members of Homo heidelbergensis. Specimens from Europe and Africa still have rather large numbers of the Australasiar, traits. Dali, Maba and Jinniushan each only have 2 of the Australasian features. Moreover, later Homo sapiens specimens from China also have a low occurrence of these features. Therefore, the region adjacent to Australasian could not have contributed to the appearance of these features in modern humans.

The presence of the Australasian traits is reduced with the appearance of Homo heidelbergensis. This is not surprising, because many of the regional features are associated with archaic features that are characteristic of Homo erectus to the exclusion of other hominins. Both Neanderthals and modern humans evolved from Homo heidelbergensis. These later species continue the reduction in Australasian traits that is begun at this time.

It is clear that Homo heidelbergensis is moving away from the features that are purported to define Australasia. However, there are no representatives of Homo heidelbergensis in the Australasian region. The temporally comparable fossil from Java
is Sambungmacan 3. This specimen only has 7 of the Australasian features, which is the same number as Kabwe. However, Kabwe has 4 absent traits, whilst Sambungmacan 3 has 0 absent features. Therefore, during the Middle Pleistocene the island of Java still has the upper hand in relation to the presence of the purported Australasian region features.

## Chapter 4--Homo neanderthalensis

## Overview

Homo neanderthalensis is a unique group of hominins that appear to be adapted to cold temperatures (Trinkaus, 1981; Holliday, 1997; Wolpoff, 1999). They were the first non-Homo sapiens hominin species to be recognized. In 1856 lime miners in Germany discovered skeletal remains in Feldhofer Grotto and these were recognized as not the same as modern humans (Tattersall, 1999). In 1864 this group was named as Homo neanderthalensis by W. King (Wood and Richmond, 2000). It has been proposed that Neanderthals evolved from European members of Homo heidelbergensis such as Petralona, Atapuerca and Steinhiem (Dean et al., 1998). They existed from 200-30kya in Europe, the Middle East and parts of western Asia (Tattersall, 2000). Neanderthal expansion into the Middle East and western Asia appears to be related to cooler periods, such that there is a fluctuation in their range related to the environmental conditions (Aiello, 1993). It seems that the arrival of modern humans in Europe around 40kya caused the eventual extinction of the Neanderthals. The latest specimens attributed to Homo neanderthalensis are from Zafarraya, Spain and date to just after 30kya. The extinction may be due to the use of the more advanced Upper Paleolithic tools by Homo sapiens (Aiello, 1993; Tattersall, 1999, 2000). Although, it does seem that some of the later Neanderthals did begin to use Upper Paleolithic tools (Mellars, 1989; Mellars, 1999). Recent genetic work appears to confirm that they are a unique species, not a subspecies of Homo sapiens (Krings et al., 1997).

It has been established that the Neanderthals are specially adapted to cold environments (Trinkaus, 1981; Holliday, 1997; Wolpoff, 1999). The Neanderthals
evidently conform to Bergmann's and Allen's rules, they have thick bones, short limbs and a deep antero-posterior chest cavity. It is theorized that their large noses warmed and moistened the cold glacial air and the prognathic mid-face allowed distance between the cold air in the nasal passages and the warm blood in the arteries supplying the brain (Wolpoff, 1999). Recent work by Holliday (1997) reveals that Homo neanderthalensis evolved in a 'hyperpolar' environment and that the closest modern human body shape to them is found in the Eskimos, not the current Northern Europeans. It seems that both extremely cold temperatures in glacial Europe and a less advanced Mousterian culture required significant biological adaptations to occur in the Neanderthals.

The Accretion Model of Neanderthal evolution appears to be the best method to describe the emergence of the classic European Neanderthals. This model comprises 4 stages that build up to the final cranial features associated with Homo neanderthalensis. According to Dean et al. (1998), the earliest stage contains 'early-pre-Neanderthals' that including Petralona and Arago. The second stage of the Accretion Model includes 'preNeanderthals' specimens such as Steinheim, Swanscombe and the finds from the Sima de los Huesos. This group shows the beginnings of the double-arched browridges and midfacial prognathism. The third stage contains 'early Neanderthals' specimens from Ehringsdorf, Saccopastore, Krapina and some of the Shanidar specimens. This stage includes the appearance of the occipital bun. The final stage represents the 'classical Neanderthals' with traits such as increased mid-facial prognathism and a deepened orbital sulcus. This last group includes Feldhofer 1, Gibraltar 1, La Chapelle-aux-saints, La Ferrassie, Amud and the other specimens form Shanidar.

Much is known about the timing and distribution of different tool traditions in Western Europe. In this region, Mousterian tools are associated with Homo neanderthalensis, Aurignacian and most other Upper Paleolithic traditions are associated with Homo sapiens, but the Chatelperronian of France, an Upper Paleolithic tradition, is associated with the Neanderthals. The appearance of the Chatelperronian demonstrates probable contact between modern humans and Neanderthals in Western Europe (Harrold, 1989; Mellars, 1989, 1999); although compare to (d'Errico et al., 1998). It should be noted that no Upper Paleolithic traditions have been found with the late surviving Neanderthals west of the Ebro river (Duarte et al., 1999; Tattersall and Schwartz, 1999). Comparing Upper Paleolithic to the Mousterian tradition, six major changes are apparent: 1) the adoption of blade technology, 2) a greater number and more complex tools, 3) use of bone, antler and ivory artifacts, 4) an explosion of symbolic artifacts, 5) improved subsistence practices and 6) changes in settlement patterns and enlarged population size (Harrold, 1989). It would seem that the Neanderthals were capable of producing extremely complex tools and only needed the stimulus of the arriving Homo sapiens.

The acculturation in tool traditions show clear contact between these two species for approximately 10 kya , but a major query revolves around the possibility of interbreeding between Neanderthals and modern humans? The Portuguese Lagar Velho 1 appears to have answered this question in a positive direction. This specimen consists of a largely complete male skeleton of about 4 years old. It has been dated to 24.5 - 25 kya , thus occurring a few thousand years later then the believed disappearance of the Neanderthals from Iberia. According to Duarte et al. (1999), this child represents a mixture of Homo sapiens and Homo neandethalensis traits that resulted from several
millennia of hybridization. This idea has been criticized, because much of the original assessment was based on inferred limb proportions. Tattersall and Schwartz (1999) assert that limb proportions are unreliable to define populations during the late Pleistocene. Unfortunately, while much of the post-cranial remains were preserved, only the left temporal bone and mandible survived. Thus, Lagar Velho 1 cannot be used in this study.

## Traits

Neanderthals possess many apomorphic features. For this investigation it is not necessary to form an exhaustive list of these traits, but only enough to clearly demonstrate that a specimen is a member of this taxa. The following information has been adapted from Stringer (1985); Trinkaus (1986); Wolpoff (1999); Wood and Richmond (2000); and personnel observations. The three traits used to establish a specimen as a Neanderthal are all apomorphies. Neanderthals display a unique double arched browridge, clear midiacial prognathism and an exclusive morphology of the posterior of the skull known as an occipital bun. These characters are scored as either present (1), absent (0), or undetermined (X).

There are many other features that are common in Neanderthals that have not been used in this analysis, two of these are the presence of a retromolar space and unique structures in the nose. A retromolar space is a clear gap between the last molar and the descending ramus of the mandible. Franciscus and Trinkaus (1995) deduced that the presence of this feature was due to the combination of a reduced dental arcade and condensed ramal breadths. It should be noted that this traits is found in some early modern humans and cannot be considered an apomorphy for Homo neanderthalensis. Schwartz and Tattersall (1996) discovered a unique arrangement in the nose of the Neanderthals that appears to be exclusive to them when compared to all other primates. The three apomorphies are a large vertical medial projection inside the internal nasal margin, the creation of a capacious posterior nasal cavity by the swelling of the lateral nasal wall and the lack of an ossified covering over the lacrimal groove. As previously described, the nose of the Neanderthals has been associated with there adaptation to the
glacial environment of Europe. Thus, these features deserve attention, even though they are not included in the cranial trait list, because of the lack of resolution on many photographs.

## Table 4-1 Homo neanderthalensis Cranial Anatomy

1. Large browridges that are arched over each orbit.
2. Mid-facial prognathism
3. Occipital bun

Table 4-2 contains all the Homo neanderthalensis specimens that will be used in this test. This list compares these fossils to the traits defined above using a presence/absence procedure. There are many more fragmentary remains available, but the author did not believe it would be advantageous to include these specimens. This decision was primarily due to the employment of a trait presence/absence technique, both for the establishment of Neanderthal status and during the exploration for Australasian characters frequency at the end of this chapter. Fragmentary remains would not add a substantial amount of diagnostic characters to the overall sample. The deviation of Tabun 1 and Amud 1 from the expected morphology will be discussed when these fossils are individually described.

Table 4-2 Homo neanderthalensis Specimens

| Characters \# | 1 | 2 | 3 | Present | Absent |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Gibraltar 1 | 1 | 1 | 1 | 3 | 0 |
| Krapina 3 | 1 | 1 | $X$ | 2 | 0 |
| La Chapelle-aux-Saints | 1 | 1 | 1 | 3 | 0 |
| Monte Circeo | 1 | 1 | 1 | 3 | 0 |
| Feldhofer 1 | 1 | $X$ | 1 | 2 | 0 |
| La Ferrassie | 1 | 1 | 1 | 3 | 0 |
| St Cesaire (p) | 1 | 1 | $X$ | 2 | 0 |
| Tabun 1 (p) | 1 | 1 | 0 | 2 | 1 |
| Shanidar 1 (p) | 1 | 1 | 1 | 3 | 0 |
| Amud 1 (p) | 1 | 1 | 0 | 2 | 1 |

Unless noted with a (p) all specimens were reviewed as casts.

## Specimens

The Gibraltar 1 cranium from Forbe's Quarry has been dated to 45-70kya (Larsen et al, 1998). The specimen is an adult cranium that is missing a large amount of its left side, including the entire left parietal and the cranial base, but the face is undamaged. It is most probably a female due to the comparatively light build of the skull. The cranial capacity is about 1200cc (Tattersall, 1999; Schwartz and Tattersall, 2002). The specimen is clearly a Neanderthal and displays all of the classical features. It displays the doublearched browridge, an occipital bun, mid-facial prognathism and an extremely large nose. According to Schwartz and Tattersall (1996), this specimen also has the apomorphic characters of the naial regions that were described above.

The Croatian site of Krapina produced Mousterian tools and several hundred fragmentary specimens including the partial cranium Krapina 3 (Tattersall, 1999). The find is dated to 130 kya (Schwartz and Tattersall, 2002). Krapina 3 lacks the cranial base, the lower face and the posterior part of the cranium, but what is preserved is clearly a Neanderthal. The browridges are thick, but not quite as arched as is normal for a Neanderthal. The preserved section of the face appears to indicate mid-facial prognathism.

The single skeleton found at La Chapelle-aux-Saints is the archetype of the classical European Neanderthal. The aged male skeleton was found in France between 1908-1911 (Tattersall, 1999; Schwartz and Tattersall, 2002). The brain size is large at approximately 1600 cc (Larsen et al., 1998). It is dated to 50 kya by faunal remains and has an ESR date of 47 and 56kya (Schwartz and Tattersall, 2002). This specimen is very well preserved, missing only a small part of the cranial base and a section of the left
parietal. As the model for the classical Neanderthals, it is not surprising that this specimen has a large, double-arched supraorbital torus, mid-facial prognathism and an occipital bun.

The Monte Circeo 1 specimen from Italy has a range of U series and ESR dates between about 60-40kya (Schwartz and Tattersall, 2002). This example comfortably fits in the Neanderthal realm. Monte Circeo 1 is a relatively complete cranium, missing part of the right maxilla and temporal bones, along with a piece of the frontal and much of the cranial base. It has a large, double-arched browridge, an occipital bun and a projecting midface. The cranial capacity is about 1550 cc (Schwartz and Tattersall, 2002).

The first Neanderthal specin_en to be recognized as a different variety of humans was Feldhofer 1. Discovered by lime miners in the Feldhofer Grotto, the skullcap represents a clear example of a Neanderthal. It has been dated to about 40 kya and has an estimated cranial capacity of 1525cc (Tattersall, 1999; Schwartz and Tattersall, 2002). The specimen consists of a frontal, both parietals and the anterior portion of the occipital. This individual had large browridges and an occipital bun.

The La Ferrassie specimens were discovered in a cave site in France. Two comparatively complete adult skeletons were recovered, along with fragmentary remains of six infants and juveniles. The site has been dated to 70kya using archaeological associations (Tattersall, 1999; Schwartz and Tattersall, 2002). La Ferrassie 1 is the most complete of the crania, missing an anterior piece of the frontal, an anterior piece of the cranial base and part of the palate. It has a brain size of 1640cc (Schwartz and Tattersall, 2002). This specimen has been reconstructed from many pieces, but preserves a clear

Neanderthal condition. The browridges are thick and arched over each orbit, the midface projects out and the rear has a clear bun on the occipital.

The St-Cesaire specimen is of supreme importance because it demonstrated that the Neanderthals produced Chatelperronian tools (Schwartz and Tattersall, 2002). This male find has been dated to 36 kya and consists of a partial cranium, a mandible and some postcranial elements (Wolpoff, 1999). The preserved parts of the crania include much of the right side of the skull, but the entire occipital, cranial base, the left parietal and left temporal are missing. The specimen displays a classical Neanderthal morphology, with a doubled arched supraorbital torus and midfacial prognathism.

The Israeli specimen Tabun 1 is an almost complete female skeleton, which appears more lightly built then the European Neanderthals. This specimen has a cranial capacity of 1271cc (Wolpoff, 1999). The site has been dated to over 100kya. The specimen has no occipital bun (Tattersall, 1999). It is not clearly understood why both Tabun 1 and Amud 1 lack an occipital bun. Otherwise, the characteristics of Neanderthal morphology are present.

Nine individuals were recovered from Shanidar cave in Iraq during excavations from 1953-1957. Shanidar $2,4,6,7,8$ and 9 are dated to 60 kya, while 1,3 and 5 have a radiocarbon date of 46 kya (Wolpoff, 1999). There are several differences between these two groups, most notable the earlier groups has more prominent zygomats and extreme anterior tooth wear. Shanidar 1, a male specimen, was included in this analysis. This find is a Neanderthal with mid-facial prognathism and a cranial capacity of 1600 cc , but it differs from the standard European morphology in some details. These elements include
reduced post-orbital constriction and a higher braincase (Wolpoff, 1999). Additionally, the maximum cranial breadth appears lower then is standard for the Neanderthals.

Amud cave, in Israel, has produced 16 Neanderthal specimens. This discovery includes a reasonably complete male skeleton, known as Amud 1 (Wolpoff, 1999). This site has been dated to $35-45 \mathrm{kya}$ (Larsen et al., 1998). Amud 1 has a cranial capacity of 1740 cc . This specimen is a Neanderthal, but it differs from the standard European morphology in several respects. The skull is high, there is no occipital bun and the browridges are reduced (Wolpoff, 1999). While the supraorbital torus is reduced in size, they still form arches over the orbits. The finds also displays projection of the middle face.

## Australasian Comparison

## Table 4-3 Australasian Features in Homo neanderthalensis

| Australasian Characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | Present | Absent |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Gibraltar 1 | 0 | 1 | $\times$ | 0 | $\times$ | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 6 |
| Krapina 3 | 0 | 1 | $X$ | $X$ | 0 | 0 | 1 | $X$ | 0 | 0 | 0 | 2 | 6 |
| La Chapelle-aux-Saints | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 8 |
| Monte Circeo | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 7 |
| Feldhofer 1 | 0 | 1 | 0 | $X$ | $X$ | $X$ | 1 | $X$ | $X$ | 0 | 0 | 2 | 4 |
| La Ferrassie | 0 | 1 | $X$ | 0 | $X$ | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 6 |
| St Cesaire (p) | 0 | 1 | $X$ | $X$ | $X$ | $X$ | 1 | 1 | $X$ | 0 | 0 | 3 | 3 |
| Tabun 1 (p) | 0 | 1 | $X$ | 0 | $X$ | $X$ | 1 | 1 | 0 | 0 | 0 | 3 | 5 |
| Shanidar 1 (p) | 0 | 1 | $X$ | 0 | $X$ | 0 | 1 | 1 | 1 | 0 | 0 | 4 | 5 |
| Amud 1 (p) | 0 | 1 | $X$ | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 7 |

Unless noted with a (p) all specimens were reviewed as casts.

The appearance of the Neanderthals represents a major leap in hominin evolution. This group had cranial capacities the same, or even slightly larger then modern humans. They are the closest group to Homo sapiens and show some features that we associate with modern humans. While Homo neanderthalensis is not on the direct line to Homo sapiens, as another closely related hominin they can still reveal information about the general trends in our lineage. There are two important things that are revealed with the investigation of the incidence of Australasian traits in Neanderthals. First, the number of features present is greatly reduced. Second, the Australasian traits that are present tend to be the same traits.

Following the pattern established by Homo heidelbergensis, the occurrence of Australasian features in the Neanderthals is reduced. The average is around 3 present and 6 absent. Interestingly, the distribution of these features is relatively stable. All of the

Neanderthals have the same three traits present. These are the occurrence of a flat, receding frontal, post-orbital constriction and facial prognathism. Only Monte Circeo and Shanidar 1 deviate from this pattern and have one extra trait each. Monte Circeo appears to have an external auditory meatus that is widest in the horizontal plane. Shanidar 1 has a relatively low maximum cranial breadth.

## Chapter 5--Homo sapiens

## Overview

The ultimate appearance of modern humans still causes great discussion in Biological Anthropology. Modern humans (Homo sapiens) appear in the fossil record sometime before 100kya. This new species displayed a unique, more gracile skeleton than its predecessor as well as many new skills as revealed by the eventual appearance of Upper Paleolithic traditions and the explosion of symbolic artifacts (Stringer and Andrews, 1988; Tattersall and Schwartz, 2000). It seems undeniable that Africa and the Middle East have the earliest modern humans, but the exact technicalities of their migration and replacement of other hominins is not entirely apparent (Stringer and Andrews, 1988; Stringer and McKie, 1996; Tattersall, 2000).

The emergence of modern humans in Africa appears to have taken several moves. Early Homo sapiens retained some archaic features, though, such traits are not grounds for dismissing these specimens as members of the modern human group. Smith (1992b) asserted that modern humans could have a few features suggestive of an archaic nature, but still be classified as members of Homo sapiens. This concept is utilized within this thesis. This early, partially archaic group includes Omo 2, LH18 and the specimens from Jebel Irhoud. Omo 2 is not used in the Australasian analysis due to an unclear providence. The calvarium appears archaic, with a low forehead, an angled occipital and a low maximum cranial breath, but it has a large cranial capacity of 1400cc (Day, 1977; Larsen et al., 1998). Rightmire (1989) stressed that this can be used to link the OmoKibish site to Homo heidelbergensis. Both Jebel Irhoud and LH18 are detailed later in
this chapter. In particular, both specimens have cranial superstructures and LH18 has a low forehead.

The appearance of totally modern humans occurred sometime before 100 kya , but these remains are fragmentary. A group of sites, Omo-Kibish, Border Cave and Klasies River Mouth, appears to represent the appearance of this complete morphology for anatomically modern humans. The major problem is that only the latter has a wellestablished date (Smith, 1992b; Wolpoff, 1999). Omo 1 is 130 kya using uraniumthorium dating of a mollusk shell, but this method is problematic (Smith, 1992; Rightmire, 1989). This specimen consists of occipital, parietal, frontal and face pieces that have been reconstructed into a cranium that is high, with small browridges (Rightmire, 1989). The stratigraphy of Border Cave is known, but the location of the Border Cave 1 find is uncertain. Matrix association has suggested a date of 90kya, but this is just an estimate (Rightmire, 1989). The Klasies River Mouth site in South Africa has produced many skeletal pieces including maxillary fragments dated to 120 kya and other pieces that originate between 100-90kya (Brauer, 1984; Brauer and Singer, 1996). Smith (1992b) and Frayer et al. (1993) claimed that remains from this site are robust and archaic, hence not modern. However, Brauer and Singer (1996) believe that all the specimens fits within the range for Homo sapiens, although some may be more robust than recent humans. Later specimens from Qafzeh and Skhul are much more complete and preserve a morphology that is clearly modern Homo sapiens. Both of these sites have been date to approximately 90 kya (Aiello, 1993).

One of the major flaws in the Multiregional hypothesis deals with the sequence that modern humans appear throughout the Earth. Homo sapiens appeared in Africa
before 100 kya. Next, they enter the Middle East around 90 kya. Subsequently, Homo sapiens remains from Liujiang indicate that moderns reached the Far East by around 60 kya . Archaeological evidence suggests that Homo sapiens entered Australasia before 40kya (Aiello, 1993). Around the same time, modern humans enter Europe. They appear to simultaneously penetrate from both the eastern and western parts of the continent (Tattersall, 1999; Tattersall and Schwartz, 2001). The last continents to be populated are the Americas. It seems extremely likely that modern humans used the Beringia land bridge between Siberia and Alaska to reach the New World. This feat was accomplished by 15 kya , but it may have occurred at an earlier date (Stringer, 1992b). If Homo sapiens evolved by a MRE model, whereby distinct regional populations are connected by gene flow, the appearance of modern humans in the already populated areas should be almost concurrent. The reality is that moderns existed in Africa for over double the amount of time they have resided in the rest of the world.

This thesis is concerned with purported Australasian features, therefore, a brief examination of this region appears prudent. Based on archaeological evidence, Australia was inhabited by 40 kya and each habitable zone on the continent was occupied by 30 kya (Jones, 1989; Aiello, 1993). The earliest securely dated skeletal remains are Lake Mungo 3, which are dated to $28-32 \mathrm{kya}$ (Brown, 2002). To get to Australia, humans would need to traverse the deep ocean trough found between the Sunda shelf (Asia) and the Sahul shelf (Australia and New Guinea). A watercraft is necessary for this trip, which includes one voyage of approximately 90 km in length. It has been theorized that this journey could have been made using bamboo rafts (Jones, 1989).

The Australian fossil record is a vital part of the Multiregional hypothesis (Thorne and Wolpoff, 1981; Wolpoff et al., 1984). While specimens from this region appear to have retained archaic features it is also possible these may be due to artificial cranial deformation. The human cranial vault is easily altered by applying force to the head within the first several years of life. This can be accomplished through the use of either pressure from the hands or with a special device. The hallmarks of artificial cranial deformation include recession of the frontal, angled parietals and a less curved occipital. Deformed frontal bones of Homo sapiens appear relatively flat, which is close to the condition found in Homo erectus (Anton and Weinstein, 1999).

There have been several studies that indicate the practice of artificial cranial deformation in Australia (Brothwell, 1975; Brown, 1989; Anton and Weinstein, 1999). The effects of this cultural custom appear to have been preserved in the fossil record. It is important to note that many of the Australian crania used in this study are probably deformed, thus the receding frontal may not be a phylogenetic link with Ngandong Homo erectus. According to Brown (1989), Kow Swamp 5, 7, Coobool Creek 49, 65 and Cohuna are deformed, while Kow Swamp 1 and Coobool Creek 16 may or may not be deformed. Anton and Weinstein (1999) assert that all the Kow Swamp specimens and Coobool Creek 65 are deformed, while Coobool Creek 16 and 49 are seen as somewhat deformed. Coobool Creek 76 was rated as undeformed by Brown (1989) and was not covered in Anton and Weinstein (1999). These results are reproduced in table 5-1, along with the author's suggestions about the status of each specimen. The criteria used to assess if a cranium was deformed involved observing if a large portion of the frontal was flat, whilst a remaining portion seems curved. This method is used because in artificially
deformed individuals the anterior two thirds of the frontal is commonly flat, while the posterior section is still curved (Brown, 1989).

Table 5-1 Artificially Deformed Specimens

| Specimens | Brown (1989) |
| :--- | :---: |
| Kow Swamp 1 | Possibly |
| Kow Swamp 5 | Yes |
| Kow Swamp 7 | Yes |
| Coobool Creek 16 | Somewhat |
| Coobool Creek 49 | Yes |
| Coobool Creek 65 | Yes |
| Coobool Creek 76 | No |
| Cohuna | Yes |


| Anton and Weinstein (1999) | Author <br> Possibly |
| :---: | :---: |
| Yes | Yes |
| Yes | Possibly |
| Yes | Yes |
| Somewhat | Yes |
| Somewhat | Yes |
| Yes | No |
| Not Reviewed | Yes |
| Not Reviewed |  |

## Traits

The features used to classify Homo sapiens were adapted from Stringer (1985); Stringer and Andrews (1988) and personnel observations. All the features are apomorphic for modern humans and include a vertical forehead, a high, short and rounded skull and weak to absent cranial superstructures. The appearance of robust superstructures on the cranium appears limited to very early modern humans from Africa (around $130-90 \mathrm{kya}$ ) and the aboriginal people from Australia. Even with the presence of some robust features all these specimens are clearly modern humans and part of the same species, Homo sapiens. These characters are scored as either present (1), absent (0), or undetermined ( X ).

One of the obvious trends that appears in recent humans is a reduction in the robusticity of the body (Stringer and Andrews, 1988; Wolpoff, 1999). It has been suggested that this trend towards gracility is partly due to the development of Upper Paleolithic tools. These novel tools reduced the strain on many elements of the human body, including the jaws and the limbs. The change in the chewing complex caused the associated muscles and structures to diminish in size. This resulted in smaller face size, especially the lower face, and the practical loss of browridges. Furthermore, lessened physical activity reduced body strength and the area of muscle attachment sites (Wolpoff, 1999).

There are several other features that are associated with modern humans. They were not included in this analysis because the three features used are clearly apomorphic and adequately represent Homo sapiens. In modern humans there is a general reduction in the amount of facial prognathism, many faces are completely tucked under the level of
the forehead. One of the most commonly cited apomorphic traits of modern humans is the presence of a chin on the mandible. A forward projection of the anterior portion of the jaw has not been found in any other hominin except Homo sapiens (Stringer and Andrews, 1988).

## Table 5-2 Homo sapiens Cranial Anatomy

1. Vertical forehead
2. General cranial shape is high, short and rounded
3. Weak to absent cranial superstructures

Table 5-3 contains all the Homo sapiens specimens that will be used in this test. This list compares these fossils to the traits defined above using a presence/absence procedure. There are more fragmentary remains available, but the author did not believe it would be advantageous to include these specimens. This decision was primarily due to the employment of a trait presence/absence technique, both for the establishment of modern human status and during the exploration for Australasian characters frequency at the end of this chapter. Fragmentary remains would not add a substantial amount of diagnostic character to the overall sample. The presence of cranial superstructures, a sloping forehead or an archaic shaped cranium will be discussed in the individual descriptions.

Table 5-3 Homo sapiens Specimens
Characters \# $1 \quad 2 \quad 3$ Present Absent

## Africa and the Middle East

| Jebel Irhoud $1(p)$ | 1 | 1 | 0 | 2 | 1 |
| :--- | :--- | :--- | :--- | :--- | :--- |
| LH $18(p)$ | 0 | 1 | 0 | 1 | 2 |
| Skhul 5 | 1 | 1 | $1^{*}$ | 3 | 0 |
| Qafzeh $6(p)$ | 1 | 1 | $1^{*}$ | 3 | 0 |
| Qafzeh $9(p)$ | 1 | 1 | 1 | 3 | 0 |
| Modern African | 1 | 1 | 1 | 3 | 0 |

## China

| Upper Cave $101(p)$ | 1 | 1 | 1 | 3 | 0 |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Upper Cave 102 (p) | 0 | 1 | 1 | 2 | 1 |
| Upper Cave 103 (p) | 1 | 1 | 1 | 3 | 0 |
| Liujiang (p) | 1 | 1 | 1 | 3 | 0 |
| Modern Asian | 1 | 1 | 1 | 3 | 0 |

## Europe

| Cro-Magnon 1 | 1 | 1 | 1 | 3 | 0 |
| :--- | :--- | :--- | :---: | :--- | :--- |
| Predmosti 3 | 1 | 1 | $1^{*}$ | 3 | 0 |
| Mladec 1 (p) | 1 | 1 | 1 | 3 | 0 |

Australasia

| Wadjak 1 | 0 | 1 | 1 | 2 | 1 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| WLH 50 (p) | 0 | 0 | $1^{\wedge}$ | 1 | 2 |
| Lake Mungo 1 (p) | 1 | 1 | 1* | 3 | 0 |
| Lake Mungo 3 (p) | 1 | 1 | 1^ | 3 | 0 |
| Kow Swamp 1 (p) | 0 | 1 |  | 2 | 1 |
| Kow Swamp 5 (p) | 0 | 1 | 1* | 2 | 1 |
| Kow Swamp 7 (p) | 0 | 1 | 1* | 2 | 1 |
| Coobool Creek 16 (p) | 0 | 1 | 1 | 2 | 1 |
| Coobool Creek 49 (p) | 0 | 1 | 1 | 2 | 1 |
| Coobool Creek 65 (p) | 0 | 1 | 1 | 2 | 1 |
| Coobool Creek 76 (p) | 1 | 1 | $1 *$ ^ | 3 | 0 |
| Cohuna (p) | 0 | 1 | 1* | 2 | 1 |
| Keilor (p) | 1 | 1 | 1 | 3 | 0 |
| Modern Australian | 1 | 1 | $1^{* \wedge}$ | 3 | 0 |

Unless noted with a (p) all specimens were reviewed as casts.
*--There is some browridge development on this specimen
$\wedge$--This specimen has some occipital crest development The modern specimens from Africa, Asia and Australia are cast produced by Bone Clones.

## Specimens

Several hominin finds from Jebel Irhoud in Morocco display a clearly modern suite of traits with some retained robusticity. The most complete specimen, Jebel Irhoud 1 , is relatively well preserved and is only missing the maxillary teeth and some of the cranial base (Day, 1977). This cranium has not been directly dated, but an associated find (Jebel Irhoud 4) has an ESR date of 130-190kya (Smith, 1992b). There is lower facial prognathism, but not to a great extent. The occipital region appears rounded, without much nuchal crest development and the general skull shape appears high and round. The face is lightly built and much smaller than earlier hominins (Smith, 1992b; Wolpoff, 1999). The cranium has one striking feature, clear browridges. According to Smith (1992b), these browridges are reduced when compared to Homo heidelbergensis. It would seem that the retained robustness of the brow is due to the early date of this specimen, not a misalignment with modern humans. The appearance of large, welldeveloped browridges in a modern human skull demonstrates the possibilities of retaining archaic features, as has been suggested for the robust Australian specimens.

Laetoli Hominid 18, also known as Ngaloba, is broadly similar to Jebel Ighoud 1 in that it retains some robusticity, but is clearly a modern human. The brain size of this specimen is small, 1200 cc , but this is still within the known range of modern human variation (Tattersall and Schwartz, 2001). This Tanzanian specimen was found in 21 fragments and dates to 129 and 108 kya based on U-series. The cranial fragments and the maxilla pieces cannot be directly joined, thus the exact attachment site must be estimated. The reconstructed cranium is missing the cranial base, both zygomats and a large portion of the maxilla, but the rest of the cranium is quite well preserved (Percy, 1996; Wolpoff,
1999). Based on the Percy (1996) reconstruction the skull is round and modern looking, with no major occipital crest development and slight lower facial prognathism. The face is small when compared to Homo heidelbergensis (Wolpoff, 1999). There are several archaic features found on this specimen, including browridge development and a relatively low forehead. The browridges are reduced when compared to earlier hominins and they are similar in shape to Omo 2 (Smith, 1992b; Wolpoff, 1999). Furthermore, while the forehead appears low, the large length of the frontal produces a relatively high cranium (Wolpoff, 1999).

The Skhul 5 cranium from Israel has been dated to around 90kya (Tattersall and Schwartz, 2001). The cranial capacity of this specimen is 1518cc (Wolpoff, 1999). It is clearly a modern human, but has mid-facial prognathism (Larsen et al., 1998). The extension of the mid face appears due to the reconstruction of this specimen. The entire mid-face, along with a small piece of the cranial base, part of the right zygomatic process of the frontal and small pieces of the right parietal and temporal are missing. Overall, the cranium is relatively high and round, but has small browridges and some development of an occipital crest. It exhibits lower facial prognathism and there is a chin on the mandible.

The Qafzeh site in Israel has produced 15 individuals that are dated to $95-90 \mathrm{kya}$. All the specimens appear modern and the crania are high and well rounded (Wolpoff, 1999). For this analysis Qafzeh 9 and 6 were chosen, because they are reasonably complete. Qafzeh 9 is a young adult, approximately 20 years old. According to Tattersall (1999) this specimen is female, but Wolpoff (1999) asserts that it is male. This individual has a relatively large cranial capacity of 1531 cc (Wolpoff, 1999). The
forehead is high and there is a lack of cranial superstructures. Conversely, Qafzeh 6 has a moderate browridge and a slightly lower forehead, but this skull still retains the general high, round shape of modern crania.

The Zhoukoudian Upper Cave site, also known as Shandingdong, has been dated to 29-34kya according to Wolpoff (1999), but Rightmire (1989) suggests a later date of 10.5-18.3kya. The discoveries from this site include 3 relatively complete crania known as $101,102,103$, along with several mandibles and isolated postcranial bones. Cranium 101 is male with a cranial capacity of 1500 cc . Cranium 102 is a teenaged male with a brainsize of 1380 cc . Cranium 103 is a female that has a brainsize of 1290 cc . All three crania have flat faces and are large, with a relatively low forehead; although 102 is clearly the lowest (Wolpoff, 1999).

The Liujiang cranium from China has a $U$ series date of 67 kya , but the relationship between the strata that was dated and the cranium's location have not been confirmed (Brown, 1992). This specimen is believed to be a young male (Wolpoff, 1999). The cranium is fully modern, but much of the associated skeletal material is robust. The face is nonprognathic, displays midline keeling and an occipital bone that is bun-shaped similar to the Homo heidelbergensis specimen Jinniushan (Wolpoff, 1999). It displays several features common in modern Asian populations including a nonprognathic 'flat' face, low nasal angle and shoveling of the lateral incisors (Etler, 1996; Wolpoff, 1999).

The first fossil representatives of modern humans in Europe were found at the Cro-Magnon rock shelter in France. Five individuals, including an infant, were discovered associated with Aurignacian tools (Tattersall, 1999). The Cro-Magnon site
has been dated by tool association to 30 kya or younger (Schwartz and Tattersall, 2002). Cro-Magnon 1 was utilized in this study due to the availability of a cast. This skull has a cranial capacity of 1600 cc (Schwartz and Tattersall, 2002). This specimen has a high and round forehead, with little browridge development (Wolpoff, 1999). It should be noted that Cro-Magnon 2 and 3 appear to display several Neanderthal-like features. Cranium 2 is a gracile female that appears to be prognathic around the midface. Cranium 3 has a lower forehead, some browridge development and a possible occipital bun (Wolpoff, 1999).

The Predmosti 3 skull from the Czech Republic has been radiocarbon dated to 26kya. The specimen has a cranial capacity of 1580 cc (Schwartz and Tattersall, 2002). While this find is clearly a modern human, there are several traits that seem to indicate a possible connection to Homo neanderthalensis. These features include the morphology of the browridges and the presence of occipital bunning (Larsen et al., 1998; Schwartz and Tattersall, 2002). Predmosti 3 is a unique find, along with the noted Neanderthal traits, the maximum cranial breadth is across the top of the mastoid processes. In addition to Predmosti 3, there are several other crania from Predmosti that display a mix of Neanderthal-like traits, including browridge development, the existence of occipital buns and low foreheads (Wolpoff, 1999).

Over 100 specimens were recovered from the Czech site of Mladec, but only a few pieces, including crania $1,2,5$ and some fragmentary cranial and post-cranial elements remain. The 1945 fire at Mikulov castle set by the retreating Nazis destroyed the other remains. Using archeological and faunal association, the site has been dated to around 32kya (Wolpoff, 1999; Schwartz and Tattersall, 2002). The original collection
included several relatively complete crania. It is believed that Mladec 1 and 2 are female, while 5 and 6 are male. Several of the crania exhibit Neanderthal-like features, including a low braincase, thick cranial bones and a structure that resembles an occipital bun (Wolpoff, 1999). Mladec 1 was used in this analysis due to its good preservation. This specimen is almost complete and clearly represents the morphology of a modern human. The braincase is high and rounded, the forehead is vertical and there are no major cranial superstructures. The mid and lower face are prognathic and there appears be a Neanderthal-like occipital bun.

Two crania and some post-cranial remains were discovered at Wadjak, Java. For this study the most complete specimen, Wadjak 1 , will be utiliced. The Wadjak 1 skull has been dated to 24-10kya (Larsen et al., 1998). This cranial capacity of this skull has been differently measured to $1475 \mathrm{cc}, 1550 \mathrm{cc}$, or 1622 cc (Storm and Nelson, 1992). The find has thickened browridge elements over the nasal area, but they laterally reduce to nothing. The forehead is low, but the frontal is curved (Wolpoff, 1999). Storm (1995) analysis of this specimen indicates that I some respects it seems to be more like the humans from Asia, rather then those from Australia.

The Kow Swamp series consists of at least forty individuals and the robust natures of these people have been used to link modern Australians to Indonesian Homo erectus (Thorne and Macumber, 1972; Thorne and Wolpoff, 1981; Wolpoff et al., 1984). This site has been radiocarbon dated to between 13-9kya (Brown, 1989). The preservation of cranial bases on all specimens is poor. All crania have thick vault bones and post-orbital constriction. Furthermore, five of the specimens have a true orbital browridge and six have occipital tori (Brown, 1989; Thorne and Macumber, 1972). Kow

Swamp 1, 5 and 7 will be used in this analysis, because they are quite complete. Kow Swamp 1 has a large browridge, a curved, receding frontal, a clear ridge of bone on the occipital, moderate post-orbital constriction and lower facial prognathism evident in the maxilla (Thorne and Macumber 1972; Larsen et al., 1998). The frontal has been described as deformed by Anton and Weinstein (1999), but reviewing photographs of this specimen the receding bone appears very curved. Therefore, I would concur with Brown (1989) that the frontal is only possibly deformed. Kow Swamp 5 has a very flat, receding forehead, a less pronounced supraorbital torus and a weak occipital torus (Thorne and Wolpoff, 1981; Storm, 1995). The Kow Swamp 5 frontal is very obviously artificially deformed. Kow Swamp 7 has a low forehead, which appears quite flat anc is clear deformed. There is some development of the browridges, but not to the extent of the previous two specimens (Brown, 2002).

The Cohuna cranium was discovered in 1925, near the edge of Kow Swamp. This find is morphologically aligned with the Kow Swamp sample (Brown, 1989). The cranium is missing a large part of the cranial base, both mastoid processes and part of the left zygomatic arch. The specimen has a flat frontal, with a high, round vault and a prognathic lower face. Only the anterior two thirds of the frontal bone are flattened, indicating artificial deformation (Brown, 1989, 2002).

The Coobool Creek series includes 126 individual and has been dated to between 14.3-7.2kya. These finds are clearly of extreme size, but there appears to be some intrapopulation variation. This population appears to be very similar to the Kow Swamp/Cohuna group (Brown, 1989; Brown 2002). For this study, crania 16, 49, 65 and 76 were used, because of the presence of published photographs of these four specimens.

It is possible that all these specimens have been artificially deformed, with the exception of Coobool Creek 76. This is clearly seen by the marked recession of the frontal. Overall, these crania are rounded and modern appearing. Coobool Creek 76 has a large orbital torus, which is separated over the nose. According to Brown (1989), there are true supraorbital tori present on Coobool Creek 28, 35, 37, 82, but photographs of these specimens have not been published.

Over 50 individuals have been found in the Willandra lakes region. Only three of these specimens, Lake Mungo 1, 3 and Willandra Lake 50 have been widely published. The Lake Mungo 1 cremation presents a single cranium that appears very gracile, with a high and curved vault, modern looking frontal, no nuchal torus and weak browrdges. The cranial base of this specimen was preserved, but it is not attached to the rest of the skull. This find has been dated to $24.5-26.5 \mathrm{kya}$. The small size of this specimen has caused great interest, but Brown noted that its size might be related to reduction due to burning (Brown, 1989, 2002). Lake Mungo 3 is an incomplete skeleton, which is missing a large amount of its skull. Only the base, right side of the vault and a piece of the face has been preserved. This specimen has been dated to 28 -32kya (Brown, 1989). Overall, Lake Mungo 3 appears to clearly be a modern human. The cranium fragments are gracile and round, with a frontal that is only slightly low and the possible development of a small browridge on the left. The cranium does have some development of an occipital crest and the maximum cranial breath is low on the skull.

One of the most discussed fossil finds from Australia has been Willandra Lakes 50. Found in 1982, this calvarium has been dated to 29 kya by ESR dating and to between 12-18kya by U series dating (Brown, 2002, Hawks et al., 2000). This specimen
may be pathological, but this claim has never been confirmed (Stringer, 1992a). The find consists of a fragmentary calvarium that is missing both temporal bones, parts of both parietals, a piece of the occipital and the entire cranial base. The skull is clearly large and robust, with a cranial capacity of 1540 cc (Brown, 2002). The major archaic features of WLH 50 include a flat, narrow and receding frontal bone, a possible supraorbital torus, a ridge of bone on the occipital and a low maximum cranial breadth around the top of the mastoids (Wolpoff, 1999).

The Keilor cranium, along with several femur fragments, was discovered in 1940 and dates vary from 12-6.8kya (Brown, 1989). The find consists of an almost complete cranium that is missing a piece of the right parietal and part of the left temporal bone. This skull appears to be modern, with a high, rounded cranium. The maxilla appears to be slightly prognathic, but not to an extreme nature. There is no development of cranial superstructures and the skull does not exhibit post-orbital constriction (Brown, 2002).

## Australasian Comparison

Table 5-4 Australasian Features in Homo sapiens

Australasian Characters

$\begin{array}{llllllllllll}1 & 2 & 3 & 4 & 6 & 7 & 8 & 9 & 1011 & \text { Present Absent }\end{array}$

## Africa and the Middle East

Jebel Irhoud 1 (p)
LH 18 (p)
Skhul 5
Qafzeh 6 (p)
Qafzeh 9 (p)
Modern African

| $0^{*}$ | 0 | $X$ | 0 | $X$ | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 7 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $0^{*}$ | 1 | $X$ | 0 | 0 | $X$ | 1 | 1 | 0 | 1 | 0 | 4 | 5 |
| $0^{*}$ | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 6 |
| $0^{*}$ | 0 | $X$ | 0 | 0 | $X$ | 1 | 1 | 0 | 0 | 0 | 2 | 7 |
| 0 | 0 | $X$ | $X$ | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 8 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |

## China

Upper Cave 101 (p)
Upper Cave 102 (p)
Upper Cave 103 (p)
Liujiang (p)
Modern Asian

| 0 | 0 | $X$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 1 | $X$ | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 8 |
| 0 | 0 | $X$ | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 8 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 9 |

## Europe

Cro-Magnon 1
Predmosti 3
Mladec 1 (p)

| 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 9 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $0^{*}$ | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 6 | 5 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 10 |

## Australasia

Wadjak 1
WLH 50 (p)
Lake Mungo 1 (p)
Lake Mungo 3 (p)
Kow Swamp 1 (p)
Kow Swamp 5 (p)
Kow Swamp 7 (p)
Coobool Creek 16 (p)
Coobool Creek 49 (p)
Coobool Creek 65 (p)
Coobool Creek 76 (p)
Cohuna (p)
Keilor (p)
Modern Australian

| $X$ | 1 | $X$ | $X$ | $X$ | 0 | 1 | 1 | 0 | 1 | 0 | 4 |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $X^{*}$ | 1 | $X$ | 1 | $X$ | $X$ | 1 | $X$ | 1 | 1 | 0 | 5 |  |
| $0^{*}$ | 0 | $X$ | 0 | $X$ | $X$ | 0 | $X$ | 0 | 0 | 0 | 0 |  |
| 0 | 0 | $X$ | 1 | $X$ | $X$ | 0 | $X$ | 1 | 0 | 0 | 2 |  |
| 1 | 1 | $X$ | 1 | $X$ | 0 | 1 | 1 | 0 | 0 | 0 | 5 | 3 |
| $0^{*}$ | $1^{\prime \prime}$ | $X$ | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 8 |
| $0^{*}$ | $1^{n}$ | $X$ | 0 | $X$ | $X$ | 1 | $X$ | 0 | 0 | 1 | 3 | 4 |
| 0 | $1^{n}$ | $X$ | 0 | $X$ | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 6 |
| 0 | $1^{n}$ | $X$ | 0 | $X$ | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 6 |
| 0 | $1^{n}$ | $X$ | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 7 |
| $0^{*}$ | 0 | $X$ | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 7 |
| $0^{*}$ | $1^{n}$ | $X$ | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 7 |
| 0 | 0 | $X$ | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 9 |
| 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 6 | 5 |

Unless noted with a (p) all specimens were reviewed as casts.
*--This specimen has a browridge, but it is not similar to those found on Ngandong
"--The frontal of this specimen is obviously, or possibly deformed

The central aim of this thesis is to elucidate the origins of modern humans. To test MRE, this work reviewed the presence of purported Australasian continuity features in the four most recent hominin species. Examination of the modern human fossil record revealed several interesting issues. The preeminent point is the general similarities between all members of the human species. The modern European and Australian fossils that respectively display possible Neanderthal traits or Indonesian Homo erectus features are not lesser members of Homo sapiens. However, this analysis reveals that it is highly probable that Australians do have a small heritage from Homo erectus from Java. This assertion is due to a combination of the earlier disappearance of robust features from Africa and a great combination of these traits in fossil Australians.

It does not appear possible for the robust features of the specimens from Kow Swamp, Coobool Creek, WLH 50 and Cohuna to be primitive retentions from an early African source. Initial modern humans in Africa do display a high combination of these traits. This combination is at a similar frequency as many of the later specimens from Australia. However, the fossils, LH 18 and Skhul 5, have been dated to just before and right after 100kya. During this time period, other African modern human have already lost almost all of the regional features. Therefore, these traits disappear in Africa 60,000 years earlier than they are found in Australia. Apart from Premosti 6, no other find from non-African regions have a high combination of Australasian features. I would suggest that this retained archaicness disappears from modern humans before they migrate out of Africa. However, if these features have been lost in modern humans, why do they appear in the Australian fossil record?

In Australia, a high percentage of the fossil record displays a large combination of the regional traits. The find with the highest frequency of traits is the modern Australian cast produced by Bone Clones. This cranium is also the only specimen that can be fully analyzed and has 6 of the 11 features. Kow Swamp 1 and WLH 50 each have 5 of the features, which is still higher then the earliest African specimens. Wadjak 1 has 4 of the features, while many of the other specimens have 3. Finally, Kow Swamp 5, Keilor and Lake Mungo 1 and 3 have between 0 to 2 traits, which is the same incidence as found in other regions. This distribution is interesting; it appears to indicate a differential expression of these features, possibly caused by a disproportion of interbreeding between Indonesian Homo erectus and the ancestors of modern Australians.

## Chapter 6-Australasian Continuity?

The objective of this examination was to review the possibility of continuity in the Australasian region and how this relates to theories about the appearance of modern humans. The first hominin to travel outside of Africa was Homo erectus and this species would be the beginning for any long-term lineages in the different regions of the world. To review the proposed continuity in Australasia, successive species of hominins were compared to an established list of these purported regional features. It is immediately clear that the suggested features are archaic and are present in all regional groups of Homo erectus. Therefore, rather than uniquely representing a lineage through time, it appears that the pattern of trait reduction is the important element. The frequency of these traits in the Australasian region stays higher than in any other area of the world. To conclusively demonstrate this assessment, the following three sections detail qualitative analysis of the distribution of trait presence/absence, quantitative analysis of the relationships of the specimens used in this study and how the dispersal of the traits possibly occurred.

## Qualitative Suggestions About Possible Lineage Continuity in Australasia

During the individual species assessments it was emphasized that there is a trend towards the reduction of Australasian features as each new hominin species appears. However, modern humans from Australasia retain more of these traits than any other group of Homo sapiens. This is clearly brought into view when the data is compiled into a single table. Tables 6-1 and 6-2 have respectively been organized by the greatest occurrence of Australasian features, and for the least number of absences. These two arrangements obviously display the unique situation for modern Australian Aborigines.

| Australasian Characters | 1 | 2 | 34 | 56 | 7 | 8 | 9 |  |  | Present | Absent |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sangiran 17 | 1 | 1 | 01 | 11 | 1 | 1 | 1 | 1 | 1 | 10 | 1 |
| Ngandong 5 | 1 | 1 | 11 | 11 | 1 | X | 1 | 1 | 1 | 10 | 0 |
| Sinanthropus reconstruction (W, 1937) | 0 | 1 | 11 | 01 | 1 | 1 | 1 | 1 | 1 | 9 | 2 |
| Ngandong 6 (p) | 1 | 1 | $\times 1$ | 11 | 1 | X | 1 | 1 | 1 | 9 | 0 |
| D2282 (p) | 1 | 1 | $\times 1$ | $1 \times$ | 1 | 1 | 1 | X | 1 | 8 | 0 |
| Sangiran 2 | X | 1 | 01 | 11 | 1 | X | 1 | 1 | 1 | 8 | 1 |
| Ngandong 1 (p) | 1 | 1 | X 1 | $1 \times$ | 1 | X | 1 | 1 | 1 | 8 | 0 |
| Ngandong 9 (p) | 1 | 1 | X 1 | 1 X | 1 | X | 1 | 1 | 1 | 8 | 0 |
| Ngandong 11 (p) | 1 | 1 | $\times 1$ | 1 X | 1 | X | 1 | 1 | 1 | 8 | 0 |
| KNM-ER 3733 | 0 | 1 | 00 | 01 | 1 | 1 | 1 | 1 | 1 | 7 | 4 |
| KNM-ER 3883 | 1 | 1 | $1 \times$ | 11 | 1 | X | 1 | 0 | 0 | 7 | 2 |
| KNM-WT 15000 | 0 | 1 | 00 | 01 | 1 | 1 | 1 | 1 | 1 | 7 | 4 |
| Sinanthropus reconstruction (T/S, 1996) | 0 | 1 | 01 | $0 \times$ | 1 | 1 | 1 | 1 | 1 | 7 | 3 |
| Sambungmacan 3 (p) | 1 | 1 | $\times 1$ | $\times 1$ | 1 | X | 1 | X | 1 | 7 | 0 |
| Ngandong 10 (p) | 0 | 1 | $\times 1$ | $1 \times$ | 1 | X | 1 | 1 | 1 | 7 | 1 |
| Kabwe | 0 | 1 | 11 | 00 | 1 | 1 | 1 | 0 | 1 | 7 | 4 |
| OH9 | 1 | 1 | $\times 1$ | $0 \times$ | 1 | X | 1 | 1 | X | 6 | 1 |
| Atapuerca 5 (Proto-Neanderthal) (p) | 0 | 1 | 01 | 00 | 1 | 1 | X | 1 | 1 | 6 | 4 |
| Predmosti 3 | 0 | 0 | 10 | 01 | 0 | 1 | 1 | 1 | 1 | 6 | 5 |
| Modern Australian | 0 | 0 | 01 | 11 | 1 | 0 | 1 | 0 | 1 | 6 | 5 |
| Hexian (p) | X | 1 | $\times 1$ | $1 \times$ | 1 | $X$ | 1 | X | $X$ | 5 | 0 |
| D2280 (p) | 0 | 1 | $\times 1$ | $1 \times$ | 1 | X | 1 | X | X | 5 | 1 |
| Ceprano (p) | 0 | 1 | X 1 | $X \times$ | 1 | X | 1 | 1 | 0 | 5 | 2 |
| Kow Swamp 1 (p) | 0 | 1 | X 1 | $\times 0$ | 1 | 1 | 0 | 0 | 0 | 5 | 3 |
| Trinil 2 | X | 1 | $\times 1$ | X X | 1 | X | X | 1 | 1 | 5 | 0 |
| Bodo (p) | 0 | 1 | $\mathrm{X} \times$ | $\times \times$ | 1 | 1 | X | 1 | 1 | 5 | 1 |
| WLH 50 (p) | X | 1 | X 1 | $X \times$ | 1 | X | 1 | 1 | 0 | 5 | 1 |
| Bou-VP-2/66 'Daka' (p) | 0 | 1 | $\times 0$ | X X | 1 | X | 1 | X | 1 | 4 | 2 |
| Petralona (p) | 0 | 1 | X 0 | 00 | 1 | 1 | 1 | X | 0 | 4 | 5 |
| Steinheim (Proto-Neanderthal) | 0 | 1 | 00 | 00 | 1 | 1 | X | 1 | 0 | 4 | 6 |
| Monte Circeo | 0 | 1 | 00 | 10 | 1 | 1 | 0 | 0 | 0 | 4 | 7 |
| Shanidar 1 (p) | 0 | 1 | $\times 0$ | $\times 0$ | 1 | 1 | 1 | 0 | 0 | 4 | 5 |
| LH 18 (p) | 0 | 1 | $\times 0$ | 0 X | 1 | 1 | 0 | 1 | 0 | 4 | 5 |
| Skhul 5 | 0 | 0 | 1 | 00 | 1 | 1 | 0 | 0 | 0 | 4 | 6 |
| Wadjak 1 | X | 1 | X X | $\times \times$ | 1 | 1 | 0 | 1 | 0 | 4 | 3 |
| Mojokerto (infant) | X | 1 | $\times 0$ | X X | 1 | X | X | 0 | 1 | 3 | 2 |
| Elandsfontein (Saldanha) | 0 | 1 | 01 | $1 \times$ X | 1 | X | X | 0 | 0 | 3 | 4 |
| Lake Ndutu (p) | X | 1 | $\times 1$ | $\mathrm{X} \times$ | X | 1 | $X$ | 0 | 0 | 3 | 2 |
| Arago 21 (p) | 0 | 1 | $\mathrm{X} \times$ | X X X | 1 | 1 | X | X | 0 | 3 | 2 |
| Gibraltar 1 | 0 | 1 | $\times 0$ | X 0 | 1 | 1 | 0 | 0 | 0 | 3 | 6 |
| La Chapelle-aux-Saints | 0 | 1 | 00 | 00 | 1 | 1 | 0 | 0 | 0 | 3 | 8 |
| La Ferrassie | 0 | 1 | X 0 | - 0 | 1 | 1 | 0 | 0 | 0 | 3 | 6 |
| St Cesaire (p) | 0 | 1 | X X | $\times \times$ | 1 | 1 | X | 0 | 0 | 3 | 3 |
| Tabun 1 (p) | 0 | 1 | $\times 0$ | O X | 1 | 1 | 0 | 0 | 0 | 3 | 5 |



Unless noted with a (p) all specimens were reviewed as casts
"--The frontal of this specimen is obviously, or possibly deformed

Once the data is arranged in descending order of the presence of Australasian features, numerous points are noticeable. First, it is obvious that Homo erectus specimens have the greatest number of these traits; representatives of this species fill the top fifteen places. Except for the more fragmentary remains, Gongwangling, EV9001, Mojokerto and Daka, all Homo erectus specimens have at least 5 of the characters. Next, the relatively robust Homo heidelbergensis has a general range of 7 to 4 , but some of the
more fragmentary remains have a reduced frequency. The Chinese members of Homo heidelbergensis are notably below this distribution. They all display only 2 of the Australasian traits, which is the top of the modern human range. Therefore, in this study the Asian representatives of Homo heidelbergensis appear more modern then their western counterparts. The Neanderthals cluster around 2 to 3 features present. Without the presence of the Australian fossil record, modern humans would display 2 to 0 of these traits. Premosti 3 has 6 of these characters, but this specimen appears quite unusual. Due to the presence of a Neanderthal-like morphology, it would appear logical to link the remarkable characters present in this specimen to intermixing with Homo neanderthalensis. Therefore, only LH18 and Skhul 5 have a moderately high frequency of 4. However, these fossils are from the very beginning of the human lineage and display an archaicness that is lost in later humans. This pattern clearly represents the slow loss of the proposed Australasian features as each successive species arises.

The Australian fossil record is unique, because it preserves modern humans with relatively high frequencies of these purported Australasian traits. The specimen with the greatest incidence of the proposed regional features is the modern cast. Both WLH 50 and Kow Swamp 1 have one less trait present with a total of 5 each. With the exclusion of Premosti 3, three specimens from Australia have a frequency of present traits greater then found in other regional populations of Homo sapiens. The African specimen, LH18 and Skhul 5 , have a frequency of 4 , which is the same as Wadjak 1. If these African crania are removed, due to the their early origins, then Kow Swamp 7, Cohuna and Coobool Creek 16, 49, 65 and 76 preserve a morphology that displays a larger occurrence of these traits compared to other modern humans. It should be noted, not all the
discoveries in Australia present a high incidence of these characters. Kow Swamp 5, Keilor and Lake Mungo 1. and 3 are within the regular range for Homo sapiens; markedly, Lake Mungo 1 has 0 of the proposed Australasian traits. Therefore, some of the fossil population from Australia is in the expected range for modern humans, whilst others are clearly above this span. There appears to be a differential expression of these regional features in modern Australians, but it is clear that, in combination, these traits do slightly represent Australasia as a region.

## Table 6-2 Number of Australasian Features Absent, Ascending

| Australasian Characters |  |  | 3 | 45 |  |  |  |  |  |  | Present | Absent |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Ngandong 5 | 1 |  | 1 | 1 | 11 | 11 | X | X 1 | 1 | 1 | 10 | 0 |
| Ngandong 6 (p) | 1 |  | X | 1 | 1 | 11 | X | X 1 | 1 | 1 | 9 | 0 |
| D2282 (p) | 1 |  | X | 1 | 1 X | X 1 | 1 | 11 |  | 1 | 8 | 0 |
| Ngandong 1 (p) | 1 |  | X | 1 | 1 X | X 1 | X | $\times 1$ |  | 1 | 8 | 0 |
| Ngandong 9 (p) | 1 |  | X | 1 | $1 \times$ | X 1 | X | X | 11 | 1 | 8 | 0 |
| Ngandong 11 (p) | 1 | 1 | X | 1 | 1 X | X 1 | X | X 1 | 1 | 1 | 8 | 0 |
| Sambungmacan 3 (p) | 1 | 1 | X | $1 \times$ | X 1 | 11 | X | $\times 1$ | X |  | 7 | 0 |
| Hexian (p) | X | 1 | X | 1 | $1 \times$ | X 1 | X | $\times 1$ | X | X | 5 | 0 |
| Trinil 2 | X |  | X | $1 \times$ | X $\times$ | $\times 1$ | X | $\times \times$ | X | 1 | 5 | 0 |
| Sangiran 17 | 1 | 1 | 0 | 11 | 11 | 11 | 1 | 11 | 1 | 1 | 10 | 1 |
| Sangiran 2 | X | 1 | 0 | 1 | 11 | 11 | X | $\times 1$ |  | 1 | 8 | 1 |
| Ngandong 10 (p) | 0 | 1 | X | 1 | $1 \times$ | $\times 1$ | X | $\times 1$ | 11 | 1 | 7 | 1 |
| OH9 | 1 | 1 | X | 1 | $0 \times$ | X 1 | X | $\times 1$ | 1 | X | 6 | 1 |
| D2280 (p) | 0 | 1 | X | 1 | $1 \times$ | X 1 | X | X 1 | X | X | 5 | 1 |
| Bodo (p) | 0 | 1 | X | X X | X X | $\times 1$ | 1 | 1 X | X | 1 | 5 | 1 |
| WLH 50 (p) | X | 1 | X | $1 \times$ | X X | $\times 1$ | X | $\times 1$ | 11 | 0 | 5 | 1 |
| Gongwangling (p) | 0 | 1 | X | X $\times$ | $\times \times$ | $\times 1$ | X | $\times \times$ | X X | x | 2 | 1 |
| EV 9001 (p) | X | 1 | X | X | X 0 | $0 \times$ | X 1 | $1 \times$ | X X | $x$ | 2 | 1 |
| Maba (p) | 0 | 1 | X | X X | X X | X 1 | X | X X |  | X | 2 | 1 |
| Sinanthropus reconstruction (W, 1937) | 0 | 1 | 1 | 1 | 0 | 11 | 1 | 11 | 1 | 1 | 9 | 2 |
| KNM-ER 3883 | 1 | 1 | 1 | X | 1 | 11 | X | $\times 1$ | 10 | 0 | 7 | 2 |
| Ceprano (p) | 0 | 1 | X | 1 | X $\times$ | $\times 1$ | X | $\times 1$ | 11 |  | 5 | 2 |
| Bou-VP-2/66 'Daka' (p) | 0 | 1 | X | 0 | X | X 1 | X | $\times 1$ | X | 1 | 4 | 2 |
| Mojokerto (infant) | X | 1 | X | 0 | X | $\times 1$ | X | $\times \times$ | $\times$ | 1 | 3 | 2 |
| Lake Ndutu (p) | X | 1 | X | 1 | X X | X $\times$ | X 1 | $1 \times$ |  |  | 3 | 2 |
| Arago 21 (p) | 0 | 1 | X | X $\times$ | X $\times$ | $\times 1$ |  | $1 \times$ |  | 0 | 3 | 2 |
| Sinanthropus reconstruction (T/S, 1996) | 0 | 1 | 0 | 1 | 0 | X |  | 11 | 1 | 1 | 7 | 3 |
| Wadjak 1 | X | 1 | X | $\mathrm{X} \times$ | $\times$ | 01 |  | 10 | 0 | 0 | 4 | 3 |
| St Cesaire (p) | 0 | 1 | X | X $\times$ | $\times$ | X | 11 | $1 \times$ | $\times$ | 0 | 3 | 3 |
| Kow Swamp 1 (p) |  | 1 | X | 1 | X | 01 | 11 | 10 | 0 | 0 | 5 | 3 |
| Atapuerca 4 (Proto-Neanderthal) (p) | X | 1 | X | 0 | 0 | $0 \times$ | X | $\times$ | $\times \times$ | X | 1 | 3 |
| KNM-ER 3733 | 0 | 1 | 0 | 0 | 0 | 1 | 11 | 11 | 11 |  | 7 | 4 |
| KNM-WT 15000 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 11 | 11 | 1 | 7 | 4 |
| Kabwe | 0 | 1 | 1 | 1 | 0 | 01 | 1 | 11 | 10 | 1 | 7 | 4 |
| Atapuerca 5 (Proto-Neanderthal) (p) |  | 1 | 0 | 1 | 0 | 0 | 1 | 1 X | $\times 1$ |  | 6 | 4 |
| Elandsfontein (Saldanha) | 0 | 1 | 0 | 1 | $\times$ | $\times$ | 1 | $\times \times$ | $\times 0$ | 0 | 3 | 4 |
| Kow Swamp 7 (p) | 0 | $1{ }^{1}$ | " X | 0 | X X | $x$ | 1 | $\times$ | 00 | 1 | 3 | 4 |
| Jinniushan (p) |  | 1 | X | 0 | X | 0 | 1 | $0 \times$ | $\times$ X |  | 2 | 4 |
| Feldhofer 1 |  | 1 | 0 | X | X | X | 1 | $\times \times$ | $\times 0$ | 0 | 2 | 4 |
| Predmosti 3 |  | 0 | 1 | 0 | 0 | 1 | 0 | 11 | 11 | 1 | 6 | 5 |
| Modern Australian |  | 0 | 0 | 1 | 1 | 1 | 1 | 01 | 10 |  | 6 | 5 |
| Petralona (p) | 0 | 1 | X | 0 | 0 | 0 | 1 | 11 | $1 \times$ |  | 4 | 5 |
| Shanidar 1 (p) |  | 1 | X | 0 | X | 0 | 1 | 11 | 10 | 0 | 4 | 5 |
| LH 18 (p) |  | 1 | $1 \times$ | 0 | $0 \times$ | X |  | 10 | 01 | 0 | 4 | 5 |


| Tabun 1 (p) |  | 1 | x | $0 \times$ | X |  |  |  |  | 0 |  |  | 3 | 5 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lake Mungo 3 (p) |  |  | X |  |  |  |  | X | 1 | 0 |  | 0 | 2 | 5 |
| Steinheim (Proto-Neanderthal) | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | X | 1 |  | 0 | 4 | 6 |
| Skhul 5 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | O |  | 0 | 4 | 6 |
| Gibraltar 1 | 0 | 1 | X | 0 | $\times$ | 0 | 1 | 1 | 0 | O |  | 0 | 3 | 6 |
| La Ferrassie |  | 1 | $\times$ | 0 | X | 0 | 1 | 1 | 0 | 0 |  | 0 | 3 | 6 |
| Coobool Creek 16 (p) | 0 | $1^{\prime \prime}$ | X | 0 | X | 0 | 1 | 1 | 0 | 0 |  | 0 | 3 | 6 |
| Coobool Creek 49 (p) | 0 | $1^{\prime \prime}$ | X | 0 | X | 0 | 1 | 1 | 0 |  |  | 0 | 3 | 6 |
| Krapina 3 | 0 | 1 | X | X | 0 | 0 | 1 | X | 0 |  |  | 0 | 2 | 6 |
| Monte Circeo | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |  | - | 0 | 4 | 7 |
| Amud 1 (p) | 0 | 1 | X | 0 | 0 | 0 | 1 | 1 | 0 |  |  | 0 | 3 | 7 |
| Coobool Creek 65 (p) | 0 | $1{ }^{\text {n }}$ | X | 0 | 0 | 0 | 1 | 1 | 0 |  |  | 0 | 3 | 7 |
| Coobool Creek 76 (p) | 0 | 0 | X | 1 | 0 | 0 | 1 | 1 | 0 |  |  | 0 | 3 | 7 |
| Cohuna (p) | 0 | 1" | X | 0 | 0 | 0 | 1 | 1 | - |  |  | 0 | 3 | 7 |
| Dali (p) | 0 | 1 | X | O | 1 | 0 | X | 0 | - |  | 0 | 0 | 2 | 7 |
| Qafzeh 6 (p) | 0 | 0 | X | 0 | 0 | X | 1 | 1 |  |  | 0 | 0 | 2 | 7 |
| Jebel Irhoud 1 (p) | 0 | 0 | X | 0 | X | 0 | 0 | 1 | - |  | 0 | 0 | 1 | 7 |
| Lake Mungo 1 (p) | 0 | 0 | X | 0 | X | $\times$ | 0 | X | - |  | 0 | 0 | 0 | 7 |
| La Chapelle-aux-Saints | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |  |  | 0 | 0 | 3 | 8 |
| Upper Cave 102 (p) | 0 | 1 | X | 0 | 0 | 0 | 0 | 1 | 1 | - | 0 | 0 | 2 | 8 |
| Upper Cave 103 (p) | 0 | 0 | X | 0 | 0 | 0 | 0 | 1 |  | 0 | 0 | 1 | 2 | 8 |
| Kow Swamp 5 (p) |  | $1{ }^{\text {n }}$ | X | $\times$ | 0 | 0 | 0 | 1 |  |  | 0 |  | 2 | 8 |
| Qafzeh 9 (p) | 0 | 0 | X | $\times$ | 0 | 0 | 0 | 1 | 1 |  | 0 |  | 2 | 9 |
| Modern Asian | 0 | 0 | 1 | 0 | 0 | 0 | 0 |  |  |  | 0 |  | 2 | 9 |
| Cro-Magnon 1 |  | 0 | 1 | 0 | 1 | 0 | 0 |  |  |  | 0 |  | 2 | 9 |
| Keilor (p) | 0 | 0 | X | - | 0 | 0 | 0 |  |  |  |  |  | 1 | 10 |
| Mladec 1 (p) |  | 0 | 0 | 0 | 0 | 0 |  |  |  |  |  |  | 1 | 10 |
| Upper Cave 101 (p) |  | 0 | X | 0 | 0 | 0 |  |  | 0 |  | 0 |  | 0 | 11 |
| Modern African | 0 | 0 | 0 | 0 | 0 | 0 |  | - | 0 |  | 0 |  | 0 | 11 |
| Liujiang (p) |  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |  | 0 | 1 |

Unless noted with a (p) all specimens were reviewed as casts
"--The frontal of this specimen is obviously, or possibly deformed

While there is a correlation between the presence of the purported regional traits and modern humans from Australia, the clearest example of the unique elements in this population is found in the frequency of absent features. The first fourteen specimens belong to Homo erectus and have 0 to 1 absent Australasian trait. Wadjak 1, WLH 50 and Kow Swamp 1 and 7 have the least number of missing traits for any modern human. Furthermore, Lake Mungo 3 and the modern Australian cast have the same frequency as

LH18. Except for Predmosti 3, the normal range for modern humans is between 7 to 11 . Skhul 5 is outside this, but it is an early African find. If the early African finds are discounted, Kow Swamp 5 and Keilor fall in the middle of the modern human scope, while Lake Mungo 1, Cohuna and Coobool Creek 16, 49, 65 and 76 are at the top of this range. Compared with the results from table 6-1, there is a differential absence of these features in the Australasian finds, whereby some are within the modern human span and others are undoubtedly outside this range.

## Quantitative Analysis of Feature Distribution

The use of a discrete character program was hoped to clearly discriminate the possible origins of modern Australians. The use of quantitative analysis was anticipated to plainly represent the qualitative suggestions that were reported above. For this investigation a program known as 'Mix' was employed (Felsenstein, 1993). This study used Wagnar parsimony, because it is unclear if the Australasian traits are truly the ancestral condition. The method permits both $0-1$ and $1-0$ changes, allowing for the reversal of features (Kluge and Farris, 1969). This program requires the use of a proposed ancestor for the start position of the tree. For this study KNM-ER 3733 was used as this ancestor, because this specimen is the earliest African Homo erectus known and has all the required features preserved.

The first series of trees that were produced used all of the specimens in this study. Unfortunately, due to the large number of fragmentary specimens, this grouping did not produce a conclusive answer. This large tree only constructed a rough separation between archaic specimens, including most of the members of Homo erectus, Kabwe, Bodo, Premosti 3, the modern Australian cast, WLH 50 and Wadjak 1, and more gracile hominins, containing most of the modern humans and the Neanderthals, with some members of Homo heidelbergensis. Thus, on this large scale three of the Australasian specimens are to some extent aligned to Homo erectus.

To help reduced the number of fragmentary specimens and possible confounding effects in this analysis, a second series of trees was produced. This grouping included the more modern Africans, the two most complete Indonesian Homo erectus specimens and
all of the relatively complete Australian finds. The favored cladogram has been reproduced in figure 6-1.

Figure 6-1 Discrete Character Analysis


The above tree plainly illustrates two facts about the origins of modern humans in Australia. First, there are two major branches of hominins, one consists of Homo erectus, while the other has all the modern humans. Second, the distribution of modern humans closely relates to the observations from the qualitative analysis. One branch of modern humans contains both Qafzeh finds, Kow Swamp 5, Keilor and Coobool Creek 76. In the
previous investigation into the presence and absence of features both Kow Swamp 5 and Keilor were within the regular range of modern humans, while Coobool Creek 76 was at the top of the modern range for absent traits. Therefore in this investigation these fossils appear to be within the modern human span. The quantitative work also re-enforces the difference between the other Australasian specimens and modern humans. The modern Australian cast, Kow Swamp 1, Cohuna and Coobool Creek 16, 49 and 65 are on separate branches from the Qafzeh group. This appears to indicate that they are not exclusively related to the African modern group.

## Potential Reasons for the Distribution of Australasian features

Reviewing fossil modern humans from Australia it has become clear that there is a unique connection between them and these proposed Australasian traits. It is also apparent that these features are present in all populations of Homo erectus. Therefore, the inquiry should review how these features originate in modern Australians? Are they retained from African modern humans, or does the Australian population have a connection to Indonesian Homo erectus? To answer these questions two separate components must be reviewed. First, the timing and distribution of these features in potential ancestors to modern humans from Australia must be established, thereby defining the populations that could live at the correct time to provide these unique traits to the migrant to Australia. Second, the distribution of these features implies certain aspects about the ancestral relationships of modern Australians.

In this analysis there are two potential sources for the ancestry of modern Australians. The first source is from African and the second one comes from the Indonesian island of Java. The Australian continent was populated sometime around 40kya (Jones, 1989; Aiello, 1993). Therefore, the two groups that can be used are an African source, using the remains from Qafzeh and the Ngandong finds from Java. The Qafzeh specimens are approximately 90kya, while the Ngandong specimens are possible as late as 27 kya (Swisher et al., 1996; Wolpoff, 1999). Both groups are slightly temporally misaligned and cannot be directly attributed as the population that migrates to Australia, but this is the best sample available. Reviewing this sample in relation to all of the Australian specimens it is clear that Australian Aborigines are modern humans, but many of them also are quite close to the Ngandong group. Therefore, this sample of
fossil modern Homo sapiens from Australia has a large connection to all modern humans, but with a small link to Indonesian Homo erectus. This appears to support a weakened Multiregional model.

It is also possible to make several hypothetical suggestions about how modern human/Homo erectus interactions occurred in Java by scrutinizing the distribution of these Australasian features in fossil Australians. In the above examinations certain fossils, Keilor, Kow Swamp 5, Coobool Creek 76 and Lake Mungo 1 and 3 were within the normal modern human range, while the others were always separate from other Homo sapiens. This would seem to indicate differential expression of features from the Indonesian Homo erectus population. Jones (1989) suggested that Australia might have been populated by a number of smaller groups, possibly blown off course traveling between some of the islands on the edge of the Sunda shelf. It would seem possible that some of these ancestral groups had a lot of contact with Indonesian Homo erectus, while others had little to none. A differential expression of Australasian traits would appear to fit the model for the colonization of the Australian continent.

## Chapter 7-Conclusion

Currently, there are two competing theories about the origins of modern humans. The Recent African Origin (RAO) model believes that modern humans originated in Africa, later migrating to the rest of the planet and causing the extinction of the other hominin species (Stringer and Andrews, 1988). The Multiregional Evolution (MRE) model asserts that modern humans arose through a complex process of regional continuity and global evolution (Wolpoff et al., 1984). A central component of the MRE theory is the use of morphologically based continuity traits, which are purported to demonstrate deep time depth for non-African regional populations. The initial effort in this thesis was to create a complete and exhaustive list of these features. This allowed a review of the validity of Australasian continuity concept to be undertaken.

This work appraised the four most recent hominins: Homo erectus, Homo heidelbergensis, Homo neanderthalensis and Homo sapiens. It was discovered that the purported Australasian traits are very common in Homo erectus and would appear to be primitive retentions from this group. There was also a clear reduction of these features through hominin evolution, leading to modern humans, which have very few of them. However, fossil Homo sapiens from Australia displayed a combination of a large presence of these traits and fewer absent features. This data was quantitatively confirmed by discrete character analysis. Thus, there is an occurrence of Australasian traits in the modern human population from Australia, as predicted by the Multiregional model. However, the source of these characters must be established.

There are two possible sources for the exceptional traits found in modern human fossils from Australia. Early modern humans in Africa display a significant number of these traits. However, this group loses many of these features before modern humans migrate out of this continent. The other possible ancestor is found in the Indonesian Homo erectus specimens from Ngandong. The best ancestral candidate for the appearance of these purported Australasian features is Homo erectus from Java.

While these purported Australasian features do characterize modern Australians, they were found in every region until quite recently. Therefore, describing them as Australasian traits seems inappropriate. Thus, the MRE suggestion of a deep lineage in Australasia does not appear correct. Rather, these features would seem better termed as evidence for brief hybridization between modern humans and Homo erectus. Furthermore, this intermixing appears to have been restricted, because none of the modern Australian remains preserve a complete morphology that is totally aligned with Homo erectus and some of the fossils are still in the range for non-Australian modern humans. More accurately, they display a mosaic of modern human features with a few archaic-looking traits.

This investigation has implications for both theories of modern human origins. A strong MRE perspective, with a deep lineage in Australasia, does not appear correct. Fossil Australians are clearly linked with modern humans. However, there are a few features that do associate them with Indonesian Homo erectus. Therefore, a strong RAO hypothesis with little to no modern/archaic intermixing also seems to be imprecise. This analysis suggests that modern human origins are a combination of an African origin, with limited interbreeding at the peripheries. This is akin to the Assimilation Model, which
was developed to represent the interactions between Neanderthals and modern humans in Europe (Smith, 1989). Future research on this topic should incorporate a more in-depth analysis of the Australasian situation compared with the European circumstances would appear relevant and appropriate. Potential work in this area of Biological Anthropology should continue with the understanding that the current condition of Homo sapiens as the only extant taxa is highly unusual. There have been clear hominin to hominin interactions in Europe and Indonesia and these factors should be included in the origins of modern humans. This analysis has demonstrated that the appearance of Homo sapiens is a complex interaction, encompassing replacement and continuity.

## References

Andrews, P. (1984). An Alternate Interpretation of Characters used to Define Homo erectus. From Cour Forsch-inst Senckenberg. 69: 167-175.

Anton, S. C. (1997). Developmental Age and Taxonomic Affinity of the Mojokerto Child, Java, Indonesia. From American Journal of Physical Anthropology. 102: 497514.

Anton, S. C. and Weinstein, K. J. (1999). Artificial Cranial Deformation and the Fossil Australians Revisited. From Journal of Human Evolution. 36: 195-209.

Arsuaga, J. L., Martinez, I., Gracia, A. and Lorenzo, C. (1997). The Sima de los Huesos Crania (Sierra de Atapuerca, Spain). A Comparative Study. From Journal of Human Evolution. 33: 219-281.

Arsuaga, J., Martinez, I., Lorenzo, C., Garcia, A., Munoz, A., Alonso, O. and Gallego, J. (1999). The Human Cranial Remains from Gran Dolina Lower Pleistocene Site (Sierra de Atapuerca, Spain). From Journal of Human Evolution. 37: 431-457.

Ascenzi, A., Mallegni, F., Manzi, G., Segre, A. G. and Naldini, E. Segre. (2000). A reappraisal of Ceprano calvaria affinities with Homo erectus, after the new reconstruction. From Journal of Human Evolution. 39: 443-450.

Asfaw, B., Gilbert, W. H., Beyene, Y., Harts, William K., Renne, P. R., WoldeGabriel, G., Vrba, E. and White, T. D. (2002). Remains of Homo erectus from Bouri, Middle Awash, Ethiopia. From Nature. 416: 317-320.

Brauer, G. (1984). A Craniological Approach to the Origins of Anatomically Modern Homo sapiens in Africa and Implications for the Appearance of Modern Europeans. From Smith, F. H. and Spencer, F. (eds). The Origins of Modern Humans: A World Survey of the Fossil Evidence. Alan R. Liss, Inc: New York, 327-410.

Brauer, G. (1989). 8.The Evolution of Modern Humans: A Comparison of the African and Non-African Evidence. From Mellars, P. and Stringer, C. (eds). The Human Revolution Behavioural and Biological Perspectives on the Origins of Modern Humans. Princeton University Press: Princeton, New Jersey, 123-154.

Brauer, G. (1992). Africa's place in the evolution of Homo sapiens. From Brauer, G. and Smith, F. H. (eds). Continuity or Replacement. A. A. Balkema: Netherlands, 83-98.

Brauer G. and Singer, R. (1996). The Klasies Zygomatic Bone: Archaic or Modern? From Journal of Human Evolution. 30: 161-165.

Brauer, G. and Stringer C. (1997). Models, Polarization, and Perspectives on Modern Human Origins. From Clark, G. A. and Willermet, C. M. (eds). Conceptual Issues in Modern Human Origins Research. Aldine de Gruyter: New York, 191-201.

Broadfield, D. C., Holloway, R. C., Mowbray, K., Silver, A., Yuan, M. S. and Marquez, S. (2001). Endocast of Sambungmacan 3 (sm3): A New Homo erectus from Indonesia. From The Anatomical Record. 262: 369-379.

Brothwell, D. (1975). Possible Evidence of a Cultural Practice Affecting Head Growth in Some Late Pleistocene East Asian and Australasian Populations. From Journal of Archaeological Science. 2: 75-77.

Brown, P. (1989). Coobool Creek, A morphological and metrical analysis of the crania, mandibles and dentitions of a prehistoric Australian human population. From Terra Australia. No. 13.

Brown, P. (1992). Recent Human Evolution in East Asia and Australasia. From Philosophical Transactions of the Royal Society of London. 337: 235-242.

Brown, P. (2000). Australian Pleistocene variation and the sex of Lake Mungo 3. From Journal of Human Evolution. 38: 743-749.

Brown, P. (2002). Peter Brown's Australian \& Asian Palaeoanthropology. From http://www-personal.une.edu.au/~pbrown3/palaeo.html.

Cann, R. L., Stoneking, M. and Wilson, A. C. (1987). Mitochondrial DNA and Human Evolution. From Nature. 325: 32-36.

Conroy, G. C., Weber, G. W., Seidler, H., Recheis, W., Nedden, D. Z. and Mariam, J. H. (2000). Endocranial Capacity of the Bodo Cranium Determined from ThreeDimensional Computed Tomography. From American Journal of Physical Anthropology. 113: 111-118.

Coon, C. S. (1962). The Origin of Races. Knopf: New York.
d'Errico, F., Zilhao, J., Julien, M., Baffier, D. and Pelegrin, J. (1998). Neanderthal Acculturation in Western Europe?: A Critical Review of the Evidence and its Interpretation. From Current Anthropology. 39: s1-s44.

Day, M. H. (3 $3^{\text {rd }}$ edition: 1977, $1^{\text {st }}$ edition: 1965). Guide to Fossil Man: A Handbook of Human Palaeontology. Cassell: London.

Day, M. H. and Stringer, C. B. (1982). A reconsideration of the Omo Kibish remains and the erectus-sapiens transition. L'Homo erectus et al Place de l'Homme de Tautavel parmi les Hominides Fossiles. Nice: Louis-Jean Scientific and Literary Publications, 2: 814-846.

Dean, D., Hublin, J., Holloway, R. and Ziegler, R. (1998). On the Phylogenetic Position of the Pre-Neanderthal Specimen from Reilingen, Germany. From Journal of Human Evolution. 34: 485-508.

Delson. E., Harvati, K., Reddy, D., Marcus, L. F., Mowbray, K., Sawyer, G. J., Jacob, T. And Marquez, S. (2001). The Sambungmacan 3 Homo erectus Calvaria: A Comparative Morphometric and Morphological Analysis. From The Anatomical Record. 262: 380397.

Dobzhansky, T., Montagu, A. and Coon C. S. (1963). Two Views of Coon's Origin of Races with Comments by Coon and Replies. From Current Anthropology. 4: 360-367.

Duarte, C., Mauricio, J., Pettitt, P. B., Souto, P., Trinkaus, E., van der Plicht, H. and Zilhao, J. (1999). The Early Upper Paleolithic Human Skeleton from the Abrigo do Lagar Velho (Portugal) and Modern Human Emergence in Iberia. From Proceedings of the National Academy of Sciences of the United States of America. 96: 7604-7609.

Etler, D. A. (1996). The Fossil Evidence for Fiuman Evolution in Asia. From Annual Review of Anthropology. 25: 257-301.

Franciscus, R. G. and Trinkaus, E. (1995). Determinants of Retromolar Space Presence in Pleistocene Homo Mandibles. From Journal of Human Evolution. 28: 577-595.

Frayer, D. W., Wolpoff, M. H., Thorne, A. G., Smith, F. H. and Pope, G. G. (1993). Theories of Modern Human Origins: The Paleontological Test. From American Anthropologist. 95: 14-50.

Freedman, L. and Lofgren, M. (1979). The Cossack Skull and a dihybrid origin of the Australian aborigines. From Nature. 8: 283-299.

Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher III, C. C., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Anton, S. C., Bosinski, G., Joris, O., Lumley, M. A., Majsuradze, G. and Mouskhelishvili, A. (2000). Earliest Pleistocene Hominid Cranial Remains from Dmanisis, Republic of Georgia: Taxonomy, Geological Setting, and Age. From Science. 288: 1019-1025.

Groves, C. P. (1989a). A Regional Approach to the Problem of the Origins of Modern Humans in Australasia. From Mellars, P. and Stringer, C. (eds). The Human Revolution, behavioural and biological perspective on the origins of modern humans. Edinburgh University Press: Edinburgh, 274-285.

Groves, C. P. (1989b). A Theory of Human and Primate Evolution. Oxford University Press: Oxford.

Grum, R. (1996). A Re-analysis of Electron Spin Resonance Dating Results Associated with the Petralona Hominid. From Journal of Human Evolution. 30: 227-241.

Grun, R. and Beaumont, P. (2001). Border Cave Revisited: a Revised ESR Chronology. From Journal of Human Evolution. 40: 467-482.

Habgood, P. J. (1985) The Origin of the Australian Aborigines: An Alternative Approach and View. From Tobias, P. V. (ed). Hominid Evolution: Past, Present and Future. Alan R. Liss Inc: New York, 367-380.

Habgood, P. J. (1989). 15.The Origin of Anatomically Modern Humans in Australasia. From Mellars, P. and Stringer, C. (eds). The Human Revolution, Behavioural and Biological Perspective on the Origins of Modern Humans. Edinburgh University Press: Edinburgh, New Jersey, 245-273

Harrold, F. B. (1989). 33.Mousterian, Chatelperronian and Early Aurignacian in Western Europe: Continuity or Discontinuity. From Mellars, P. and Stringer, C. (eds). The Human Revolution, Behavioural and Biological Perspective on the Origins of Modern Humans. Edinburgh University Press: Edinburgh, New Jersey, 677-713.

Hawks, J., Oh, S., Hunley, K., Dobson, S., Cabana, G., Dayalu, P. and Wolpoff, M. H. (2000). An Australasian test of the recent African origin theory using the WLH-50 calvarium. From Journal of Human Evolution. 39: 1-22.

Holliday, T. W. (1997). Postcranial Evidence of Cold Adaptation in European Neanderthals. From American Journal of Physical Anthropology. 104: 245-258.

Howell, F. C. (1960). European and Northwest African Middle Pleistocene Hominids. From Current Anthropology. 1: 195-232.

Jones, R. (1989). 35.East of Wallace's Line: Issues and Problems in the Colonization of the Australian Continent. From Mellars, P. and Stringer, C. (eds). The Human Revolution, Behavioural and Biological Perspective on the Origins of Modern Humans. Edinburgh University Press: Edinburgh, New Jersey, 743-782.

Jorde, L. B., Bamshad, M. and Rogers, A. R. (1998). Using mitochondrial and nuclear markers to reconstruct human evolution. From BioEssays. 20: 126-136.

Jurmain, R., Nelson, H., Kilgore, L. and Trevathan, W. (2001). Essentials of Physical Anthropology. Wadsworth: Belmont.

Krings, M., Stone, A., Schmitz, R. W., Krainitzki, H., Stoneking, M. and Pabo, S. Neandertal DNA Sequences and the Origin of Modern Humans. From Cell. 30: 19-30.

Lahr, M. M. (1994). The Multiregional Model of modern human origins: a reassessment of its morphological basis. From Journal of Human Evolution. 26: 23-56.

Laitman, J. T. and Tattersall, I. (2001). Homo erectus newporkensis: An Indonesian Fossil Rediscovered in Manhattan Sheds Light on the Middle Phase of Human Evolution. From The Anatomical Record. 262: 341-343

Lambert, D. M. and Spencer, H. G. (eds). (1995). Speciation and the Recognition Concept, Theory and Application. The John Hopkins University Press: Baltimore and London.

Larnach, S. L. and Macintosh, N. W. G. (1974). A Comparative Study of Solo and Australian Aboriginal Crania. From Elkin, A. P. and Macintosh, N. W. G. (eds). Grafton Elliot Smith, the Man and His Work. Sydney University Press: Sydney, 95-102.

Larsen, C. S., Matter, R. M. and Gebo, D. L. (1998). Human Origins The Fossil Record. Waveland Press Inc: Prospect Heights, Illinois.

Leakey, L. S. B. (1963). East African Fossil Hominoidea and the Classification within this Super-Family. From Washburn, S. L. (ed). Classifications and Human Evolution. Publications in Anthropology, No. 37. Viking Fund: New York, 32-4\%.

Lewin, R. (1989). Species Questions in Modern Human Origins. From Science. 243(4899): 1666-1667.

Macintosh, N.W.G. (1967). Fossil Man in Australia. From Australian Journal of Science. 30:86-98.

Marquez, S., Mowbray, K., Sawyer, G. J., Jacob, T. and Silvers, A. (2001). New Fossil Hominid Calvaria from Indonesia. 262: 344-368.

Nitecki, M. H. and Nitecki, D. V. (eds). Origins of Anatomically Modern Humans. Plenum Press: New York and London, 175-199.

Paterson, H. E. H. (1978). More Evidence against speciation by reinforcement. From South African Journal of Science. 74: 369-371.

Rightmire, G. P. (1988). Homo erectus and Later Middle Pleistocene Humans. From Annual Review of Anthropology. 17: 239-259.

Rightmire, G. P. (1989). 7.Middle Stone Age Humans from Eastern and Southern Africa. From Mellars, P. and Stringer, C. (eds). The Human Revolution Behavioural and Biological Perspectives on the Origins of Modern Humans. Princeton University Press: Princeton, New Jersey, 109-122.

Rightmire, G. P. (1990). The Evolution of Homo erectus: comparative and anatomical studies of an extinct human species. Cambridge University Press: Cambridge.

Rightmire, G. P. (1996). The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? From Joumal of Human Evolution. 31: 21-39.

Rightmire, G. P. (1998a). Human Evolution in the Middle Pleistocene: The Role of Homo heidelbergensis. From Evolutionary Anthropology. 6: 218-227.

Rightmire, G. P. (1998b). Evidence From Facial Morphology for Similarity of Asian and African Representatives of Homo erectus. From American Journal of Physical Anthropology. 106: 61-85.

Schwartz, J. H. and Tattersall, I. (1996). Significance of Some Previously Unrecognized Apomorphies in the Nasal Region of Homo neanderthalensis. From Proceedings of the National Academy of Sciences of the United States of America. 93: 10852-10854.

Schwartz, J. H., and Tattersall, I. (2002). The Human Fossil Record. Volume 1: Terminology and Craniodental Morphology of Genus Homo (Europe). Wiley-Liss: New York.

Seidler, H., Falk, D., Stringer, C., Wilfing, H., Muller, G., Nedden, D. Z., Weber, G. W., Reicheis, W. and Arsuaga, J. (1997). A Comparative Study of Stereolithographically Modelled Skulls of Petralona and Broken Hill: Implications for Future Studies of Middle Pleistocene Hominid Evolution. From Journal of Human Evolution. 33: 691-703.

Shapiro, H. L. (1974). Peking Man, the Discovery, Disappearance and Mystery of a Priceless Scientific Treasure. Simon and Schuster: New York.

Shipman, P. (2001). The Man Who Found the Missing Link. Simon and Schuster: New York, London, Toronto, Sydney, Singapore.

Sigmon, B. A. and Cybulski, J. S. (eds). (1981). Homo erectus Papers in Honor of Davidson Black. University of Toronto Press: Toronto, Buffalo, London.

Smith, F. H. (1984). Fossil Hominids From the Upper Pleistocene of Central Europe and the Origins of Modern Europeans. From Smith, F. H. and Spencer, F. (eds). The Origins of Modern Humans: A World Survey of the Fossil Evidence. Alan R. Liss, Inc: New York, 137-209.

Smith, F. H. (1992a). The Role of Continuity in Modern Human Origins. From Brauer, G. and Smith, F. H. (eds). Continuity or Replacement. A. A. Balkema: Netherlands, 145156.

Smith, F. H. (1992b). Models and Realities in Modern Human Origins: The African Fossil Evidence. From Philosophical Transactions: Biological Sciences. 337(1280): 243-250.

Smith, F. H., Falsetti, Anthony B. and Donnelly, Steven M. (1989). Modern Human Origins. From Yearbook of Physical Anthropology. 32: 35-68.

Strom, P. (1995). The Evolutionary Significance of the Wajak Skulls. From Scripta Geological. 110: 1-247.

Strom, P., and Nelson, A. (1992). The Many Faces of Wadjak Man. From Archaeology in Oceania. 27: 37-46.

Stringer, C. B. (1984). The Definition of Homo erectus and the Existence of the species in Africa and Europe. From Courier Forschungs-Institut Senckengberg. 69: 131-143.

Stringer, C. B. (1985). Middle Pleistocene Hominid Variability and the Origins of Late Pleistocene Humans. From Delson, E. (ed). Ancestors: the Hard Evidence. Alan R. Liss Inc: New York, 289-295.

Stringer, C. B. (1987). A Numerical Cladistic Analysis for the Genus Homo. From Journal of Human Evolution. 16: 135-146.

Stringer, C. B. (1992a). Replacement, Continuity and the Origin of Homo sapiens. From Brauer, G. and Smith, F. H. (eds). Continuity or Replacement. A. A. Balkema: Netherlands, 9-24.

Stringer, C. B. (1992b). 6.6 Evolution of early humans. In Jones, S., Martin, R., Pilbeam. and Bunney, S. (eds). The Cambridge Encyclopedia of Human Evolution. Cambridge University Press: Cambridge, 241-251.

Stringer, C. B. (1994). Out of Africa-A Personal History. From Nitecki, M. H. and Nitecki, D. V. (eds). Origins of Anatomically Modern Humans. Plenum Press: New York and London, 149-172.

Stringer, C. B. and Andrews P. (1988). Genetic and Fossil Evidence for the Origin of Modern Humans. From Science. 239: 1263-1268.

Stringer, C. and Brauer, G. (1994). Methods, Misreadings, and Bias. From American Anthropologist. 96: 416-424.

Stringer, C. and McKie, R. (1996). African Exodus, The Origins of Modern Humans. A John Macrae/Owl Book, Henry Holt and Company: New York.

Stoneking, M., Bhatia, K. and Wilson A. C. (1986). Rate of Sequence Divergence Estimated from Restricted Maps of Mitochondrial DNAs from Papua New Guinea. From Cold Springs Harbor Symposia on Quantitative Biology. 51: 433-439.

Stoneking, Mark. and Cann, Rebecca L. (1989). African Origin of Human Mitochondrial DNA. From Mellars, P. and Stringer C. (eds). The Human Revolution. Edinburgh University Press: Scotland, 17-30.

Swisher, C. C., Curtis, G. H., Jacob, T., Getty, A. G., Suprijo, A. and Wildasmoro. (1994). Age of the Earliest Known Hominids in Java, Indonesia. From Science. 263: 1118-1121.

Swisher III, C. C., Rinks, W. J., Anton, S. C., Schwarcz, H. P., Curtis, G. H., Suprijo, A. and Widiasmoro. (1996). Latest Homo erectus of Java: Potential Contemporaneity with Homo sapiens in Southeast Asia. From Science. 274: 1870-2874.

Swisher III, Carl C., Curtis, Garniss H. and Lewin, Roger. (2000). Java Man. Scribner: New York, London, Toronto, Sydney and Singapore.

Tattersall, I. (1999). The Last Neanderthal. A Peter N. Nevraumont Book, Westview Press, A member of the Perseus Books Group: New York.

Tattersall, I. (2000). Paleoanthropology: The Last Half-Century. From Evolutionary Anthropology. 9: 2-16.

Tattersall, I. and Sawyer, G. J. (1996). The Skull of "Sinanthropus" from Zhoukoudian, China: a new reconstruction. From Journal of Human Evolution. 31: 311-314.

Tattersall, I. and Schwartz, J. H. (1998). Morphology, Paleoanthropology, and Neanderthals. From The Anatomical Record. 253: 113-117.

Tattersall, I. and Schwartz, J. H. (1999). Hominids and Hybrids: The Place of Neanderthals in Human Evolution. From Proceedings of the National Academy of Sciences of the United States of America. 96: 7117-7119.

Tattersall, I. and Schwartz, J. H. (2000) Extinct Humans. Westview press: Colorado.
Templeton, A. R. (1993). The "Eve" Hypotheses: A Genetic Critique and Reanalysis. From American Anthropologist. 95: 14-50.

Thorne, A. G. (1977). Separation or Reconciliation? Biological Clues to the Development of Australian Society. From Allen, J. Golson, J. and Jones, R. (eds). Sunda and Sahul, Prehistoric Studies in Southeast Asia, Melanesia and Australia. Academic Press: London, New York and San Francisco, 187-204.

Thorne, A. G. and Macumber, P. G. (1972). Discoveries of Late Pleistocene Man at Kow Swamp, Australia. From Nature. 238: 316-319.

Thorne, A. G. and Wolpoff, M. H. (1981). Regional Continuity in Australasian Pleistocene Hominid Evolution. From American Journal of Physical Anthropology. 55: 337-349.

Thorne, A. G. and Wolpoff, M. H. (1992). The Multiregional Evolution of Humans. From Scientific American. 63: 76-83.

Trinkaus, E. (1981). Neanderthal Limb Proportions and Cold Adaptations. From Stringer C. B. (ed). Aspects of Human Evolution. Taylor and Francis: London, 187-224.

Trinkaus, E. (1986). The Neanderthals and Modern Human Origins. From Annual Review of Anthropology. 15: 193-218.

Underhill, P. A. Passarino, G. Lin, A. A. Shen, P. Lahr, M. M. Foley, R. A. Oefner, P. J. and Cavalli-Sforza, L. L. (2001). The Phylogeography of Y Chromosome binary haplotypes and the Origins of Modern Human Populations. From Annual of Human Genetics. 61: 43-62.

Weidenreich, F. (1937). Reconstruction of the entire skull of an adult female individual of Sinanthropus pekinensis. From Nature. 140: 1110-1111.

Weidenreich, F. (1943). The skull of Sinanthropus Pekinensis; A Comparative Study on a Primitive Hominid Skull. From Palaeontologia Sinica. New Series D, 10: 1-484.

Weidenreich, F. (1946). Apes, Giants and Man. The University of Chicago Press: Chicago, London.

Weidenreich, F. (1949). Generic, Specific and Subspecific Characters in Human Evolution. From American Journal of Physical Anthropology. Volume 4, December, 1946. Reprinted in The Shorter Anthropological Papers of Franz Weidenreich Published in the Period 1939-1948, A Memorial Volume. Compiled by Washburn, S. L. and Wolffson, D. The Viking Fund Inc: New York.

Weidenreich, F. (1951). Morphology of Solo Man. From Anthropological Papers of the American Museum of Natural History. 43: 207-290.

Wheeler, Q., and Meier, R. (eds). (2000). Species Concepts and Phylogenetic Theory. Columbia University Press: New York.

Wilson, R. A. (ed). (1999). Species, New Interdisciplinary Essays. MIT Press: Cambridge and London.

Wood, B. A. (1991). Koobi Fora Research Project. Hominid Remains. Vol 4. Clarendon Press: Oxford.

Wood, B. (1994). Taxonomy and Evolutionary Relationships of Homo erectus. From Courier Forschungs-Institut Senckengberg. 171: 159-165.

Wolpoff, M. H. (1985). Human Evolution at the Peripheries: The Pattern at the Eastern Edge. From Tobias, P. V. (ed). Hominid Evolution: Past, Present and Future. Alan R. Liss Inc: New York, 355-365

Wolpoff, M. H. (1989). Multiregional Evolution: The Fossil Alternative to Eden. From Mellars, P. and Stringer C. (eds). The Human Revolution. Edinburgh University Press: Scotland, 62-108.

Wolpoff, M. H. (1992) Theories of Modern Human Origins. From Brauer, G. and Smith, F. H. (eds). Continuity or Replacement. A. A. Balkema: Netherlands, 25-63.

Wolpoff, M. H. (2 ${ }^{\text {nd }}$ ed:1999, $1^{\text {st }}$ ed:1980). Paleoanthropology. McGraw-Hill: Boston, Burr Ridge, Dubuque, Madison, New York, San Francisco, and St Louis.

Wolpoff, M. H., Xin Zhi, W. and Thorne, A. G. (1984). Modern Homo sapiens Origins: A General Theory of Hominid Evolution Involving the Fossil Evidence From East Asia. From Smith, F. H. and Spencer, F. (eds). The Origins of Modern Humans: A World Survey of the Fossil Evidence. Alan R. Liss, Inc: New York, 411-483.

Wolpoff, M. H., Thorne, A. G., Smith, F. H., Frayer, D. W. and Pope, G. G. (1994). Multiregional Evolution: A Worldwide Source for Modern Human Populations. From Nitecki, M. H. and Nitecki, D. V. (eds). Origins of Anatomically Modern Humans. Plenum Press: New York and London, 175-199.

Wolpoff, M. and Caspari, R. (1997a). What Does it Mean to be Modern? From Clark, G. A. and Willermet, C. M. (eds). Conceptual Issues in Modern Human Origins Research. Aldine de Gruyter: New York, 28-44

Wolpoff, M. and Caspari, R. (1997b). Race and Human Evolution. Simon and Schuster: New York.

Wolpoff, M. Hawks, J. and Caspari, R. (2000). Multiregional, Not Multiple Origins. From American Journal of Physical Anthropology. 112: 129-136.

Wood, B. and Richmond, B. G. (2000). Human Evolution: Taxonomy and Paleobiology. From Journal of Anatomy. 196: 19-60.

