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The mark of Ancient Java is on none of them

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Abstract

The mark of Ancient Java refers to the persistence of *Homo erectus* traits from Javan populations in fossil *Homo sapiens* Australian crania. This paper argues that hybridization of these two species is unlikely, first because the evidence for chronological overlap is very weak and second because phylogenetic analysis (cladistics and splits network) incorporating the earliest fossils of modern humans from Africa and the Levant indicate no close genetic relationship between a Ngandong-like population from Java and 26 late Pleistocene Australian fossils from the Willandra Lakes.

Since the initial palaeoanthropological research of Weidenreich (1943, 1945 and 1946), there has been much emphasis on the role of *Homo erectus* from Indonesia (or Sunda) in the peopling of Ancient Australia (or Sahul). In a 1965 summary of the known Australasian human fossil series of the time, which included Talgai, Mossgiel, Cohuna, Keilor and Aitape, Macintosh noted:

> The mark of ancient Java is on all of them, but that can be seen in modern Aboriginal crania too. All show individual or combined features which can be spoken of as primitive: and a morphological sequence can be detected ranging from Talgai, at the more primitive extreme, through Mossgiel (tentatively), Cohuna, Tartanga, and finally the most modern-looking Keilor. (Macintosh 1965: 59)

He observed that Cohuna, Talgai and Mossgiel had certain morphological similarities that set them apart from Keilor. The results of his initial study indicated that there was indeed a link between the Australian fossil record and fossil forms from Java (Macintosh 1967). Later with his colleague Larnach (Larnach and Macintosh 1974, Macintosh and Larnach 1976: 118) he was to withdraw his claim of a close phylogenetic link between *Homo erectus* in Java and the Aboriginal Australians. Following a study of the Ngandong crania, Macintosh and Larnach (1974, 1976) argued that the great morphological differences of *Homo erectus* compared to modern Aboriginal crania, and the presence of unique features in the erectines, made it extremely unlikely that Ngandong was ancestral to Australians. It would seem however, that the seed was sown.

The quest was to be taken up enthusiastically by Macintosh's then PhD student Alan Thorne in the late 1960s. Thorne was to dramatically increase the fossil human sample in Australia; his important excavations at Kow Swamp increased the number from 5 (Talgai, Cohuna, Keilor, Lake Nitchie and Mossgiel) to 27. For the first time, there was a significant series of fossil remains from a single locality, and many of these retained a very robust cranial morphology. In March 1969 Jim Bowler, John Mulvaney, Rhys Jones, and Harry Allan from the ANU were to excavate the remains of a young female (WLH 1, known as Mungo Lady) from the ancient shores of Lake Mungo on the property of Joulni; the morphology of these remains was quite distinct from the more robust crania recovered from Kow Swamp. Further gracile remains, this time of a male (WLH 3) were recovered from a location only 400 m north of the Mungo Lady site. The fossils at Lake Mungo appeared to provide quite a different morphology from that at Kow Swamp, more comparable to the 'modern-looking' Keilor skull, and this disparity generated the Di-hybrid model, which argued that two distinct populations were responsible for the colonisation of Australia (Thorne, 1976). Unlike Birdsell's controversial Tri-hybrid model, Thorne's model was able to draw upon an extensive series of fossil human remains, a series that Thorne had himself largely recovered and painstakingly reconstructed.

A large amount of research since Thorne's initial work has illustrated that the variation within Sahul has no close biological link with the archaic populations from Sunda and are representative of phenotypic variation within a single population. For example Habgood (1991), following Wolpoff (1980), has noted that the variation in Pleistocene crania can be explained within a single homogenous population. He notes that two of the main Australian late Pleistocene samples (Kow Swamp and Coobool Creek) contain specimens representing both ends of the morphological spectrum, and numerous intermediates. Habgood (1985 and 1986) further demonstrated through multivariate analysis that the robust and gracile groups within the broader Australian Pleistocene sequences are more similar to each other than to specimens from other geographic regions.

A number of publications still contend that Pleistocene Australians are, at least in part, derived from ancient Javan *Homo erectus* populations, the most significant recent publications being those of Hawks *et al*. (2001), Webb (2006), and Curnoe (2007). However Curnoe (2009) has

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more recently changed his views and now accepts a purely modern *Homo sapiens* origin for the first Australians.

The earliest specimens of *Homo sapiens* derive from East Africa, at sites such as Herto and Omo, strongly suggesting that modern human morphology evolved in Africa (White *et al.* 2003 and McDougal *et al.* 2005), not in Europe or Asia. Until such time as fossils of anatomically modern humans dating to before 200,000 years are found in Asia or Europe this remains the most plausible hypothesis.

The major question we investigate in this paper is the plausibility of admixture or assimilation of archaic populations by modern humans migrating through the Sunda chain. The possibility of hybridisation in Europe and the Levant between *Homo neanderthalensis* and *Homo sapiens* has been debated for some time now. Some fossils have been proposed as demonstrating evidence of admixture, although all have been dismissed following further scrutiny (Klein 2008 for a discussion). As the chronology for *Homo sapiens* and Neanderthals has been refined, it appears that the period of actual overlap between the two species is perhaps not as long as initially thought (Finlayson 2004). Establishing reliable chronologies for the two species therefore has been an important aspect of investigating the question of admixture in Europe.

In this paper we would like to review the possibility of admixture between *Homo erectus* and *Homo sapiens*, which was first raised in a late change of heart by Weidenreich (according to Birdsell 1967) and further considered by Howell (1973). It is impossible to consider the question of hybridisation of archaic humans in Sunda by moderns without first considering the antiquity of the site of Ngandong. We will do so by briefly addressing the question of contemporaneity between *Homo erectus* and *Homo sapiens* in Java, as proposed by recent dates for the site of Ngandong. If there is evidence for considerable temporal overlap between the two species this would at least provide the opportunity for admixture.

The paper will then compare the morphology of the earliest known specimens of *Homo sapiens* with *Homo erectus* and the earliest known fossil sequence of modern humans from Australia, from the Willandra Lakes region, in order to establish if there is a 'mark of Ancient Java' indicating assimilation of *Homo erectus* by modern humans. As the Kow Swamp series has been reburied, the Willandra series with its great range of cranial diversity (Webb 1989 and 2006) now provides the best opportunity to assess the question of hybridisation.

In human palaeontology the application of fundamental morphological comparison is still commonplace. This is particularly the case in Australia (see for example Webb 2006). The application of phylogenetic systematics provides a more objective means of making such assessments and establishing the frequency of common ancestors in the fossil hominin from the late Pleistocene period. For this, we first need to be able to identify those similarities that result from common ancestry. This is done by identifying similar character states that are shared between the fossil specimens. A character can be defined as a feature, or perhaps more accurately a unit of heritable information, passed from an ancestor to a descendant; a state is one (of two or more) form which a character can exhibit (Lieberman 2000: 88). Recognising homologies is central to this approach. Homologies are similarities in anatomical structures, between specimens, that have a phylogenetic origin (Lieberman 2000: 87). They can be either ancestral states, termed plesiomorphic, or derived (descendant) states, termed apomorphic. Determining what are plesiomorphic and what are apomorphic states is central to phylogenetic systematics and is termed character polarisation (Cameron and Groves 2004: 107). Characters can also have a direct functional component and as a result there has been considerable discussion around what influence environment (including factors such as increased loading) may have on their expression (e.g. Lieberman 1995 and Bräuer *et al.* 2004).

Cladistics has been applied successfully in palaeontology to resolve questions of evolutionary relationship for numerous fossil taxa, but its application came rather late to palaeoanthropology (Groves 1989: 213). Depending of course on sample sizes, its application is more accurate over longer geological time scales than shorter ones. Speciation events in large vertebrate taxa tend to occur over long periods of time. An example of the successful application of cladistics to arrange fossil taxa over a long geological time scale is the division of fossil taxa into clades such as *Paranthropus*, *Australopithecus* and *Homo*; cladistic analysis has demonstrated that there is more than one genus in the tribe Hominini and that the prime candidate for generic speciation was likely to be *Paranthropus* (Groves 1989: 215–227). The identification of cladistic relationships at a whole organism level can therefore be expected in the analysis of samples undertaken on very well separated species.

While cladistics will classify the most parsimonious evolutionary relationship between species by forcing the data into a tree-shaped diagram, it will not provide an appreciation of the relationship between closely related species. If species are not sufficiently separated it is therefore unlikely that we will be able to obtain any insights into the evolutionary relationships amongst fossil taxa other than separating specimens that do not belong to the sapient clade. Therefore another technique will be employed to explore the possibility of genetic exchange between species that may result in hybridisation. Splits network (Huson and Bryant 2006) is a newly developed phylogenetic program designed to explore multiple possible links between different taxa in order to begin examining questions such as hybridisation of species. It has not yet been applied in the field of palaeoanthropology and is trialled here in order to see if it is in agreement with the cladistic analysis.

The age of late *Homo erectus* at Ngandong, Java

Crucial to understanding the feasibility of the hybridisation model for Sunda and Sahul is resolving the question of chronological overlap between *Homo erectus* and *Homo sapiens*. Indeed it is difficult to review a model for the colonisation of Australia by a *Homo erectus*-derived population such as the Ngandong people from Central Java without considering the age of the site. Although one of us will consider this in more detail elsewhere (Westaway, in prep), we will summarise the general position here.

An antiquity for *Homo erectus* at Ngandong as late as 27,000 BP has been proposed (Swisher *et al*. 1996). Taken into conjunction with the likelihood that modern humans have been in Australia for at least 50,000 years (Bowler *et al*. 2003), this suggests that there may have been coexistence between the two species in Sunda for at least 23,000 years, providing an opportunity for admixture. Problems have been identified with the late dates for Ngandong by a number of researchers (Grün and Thorne 1997, Van Den Bergh 1999, Storm 2001 and Westaway 2002); despite this the late dates are often cited in more general palaeoanthropological accounts (e.g. Cameron and Groves 2004, Stringer and Andrews 2005, Lockwood 2008). The subsequent discovery of *Homo floresiensis* (Brown *et al*. 2004, Morwood *et al*. 2004) has further bolstered the possibility that there were sympatric species of hominins in Sunda. While careful excavation has revealed a clear stratigraphic sequence and chronology for *Homo floresiensis*, this has not always been the case for *Homo erectus* at Ngandong.

In order to establish an age range for Ngandong Swisher *et al.* (1996) applied Uranium series/ESR dating to faunal remains from Ngandong either excavated during their project or already held in museum collections. The museum collections that were dated included a specimen excavated between 1931 and 1933 by the Dutch East Indies Geological Survey and held at the Geological Research and Development Centre (GRDC) in Bandung, and specimens held at Gadjah Mada University (GMU) in Yogyakarta, excavated by Jacob between 1976 and 1980. These specimens were collected from site 1, which is the location of the *Homo erectus* material, and site 2, excavated by Jacob. Site 2 is located several hundred metres upstream from site 1 and has not yet produced any fossils that have been clearly described as being from *Homo erectus*. The new non-hominin fossil material excavated and dated by Swisher *et al.* (1996) came from an area they believed to be adjacent to the excavation directed by Oppenoorth and Ter Haar between 1931 and 1933.

Further faunal remains from two additional sites along the Solo River yielded similar ages to the dates Swisher acquired from Ngandong. There are two dates from a single tooth with a median range of 27 to 40 ky from Jigar, located several kilometres downstream from Ngandong, and a single date with a median age range of 32 to 53 ka obtained from Sambungmacan (Sm), which is more than 50 km upstream. Fossil material from the latter locality has been recovered from an area spread over several kilometres and from available accounts the depositional time span of the fossil-bearing strata, including the human fossils, is far from clear (Aziz et al 2004). Sm1 and Sm4 have been recently interpreted as showing intermediate features between the Ngandong specimens and the much earlier Sangiran specimens, although Sm 3 is considered to demonstrate morphological similarity with the Ngandong specimens (Aziz *et al.* 2004; Baba *et al.* 2004). Fluorine counts from a tibial shaft (Sm2) and some undated Ngandong faunal remains are similar, suggesting that some elements from these sites may be of a similar age (Jacob 1981). A U-series date from a bovid tooth of uncertain provenance from Sambungmacan with a median range of 32 to 53 ka is considered by Swisher et al (1996) to provide an age for the Sambungmacan hominins.

The Ngandong dates have been contested on the grounds of the reliability of the dating technique employed (Antón 2001, Grün and Thorne 1997). It has been suggested that there may be a systematic error in the U-series/ESR technique on tooth and bone that could repeatedly produce inaccurate ages (Antón 2001). It is now clear that open bone does not provide a stable environment for uranium, and migration in and out of the bone (i.e. the mobility of uranium) has been identified as a major limiting factor in U-series dating in open environments (Grün 2006:14). Furthermore changing hydrological systems have the potential to create fluctuations in the U-uptake in bone (Grün 2006: 12). At present the hydrological history at Ngandong is not well established and is likely to be complex. More accurate U-series analysis of bone requires calibration against matrix matched standards with known Th/U ratios (Eggins *et al.* 2005) and it is uncertain whether calibration at Ngandong was undertaken by Swisher *et al.* on the sediments from the Dutch excavations. The development of laser ablation-MC-ICPMS for U-series dating adds the potential for further refinement of dates as it can be employed to better understand open system behaviour in bone and potentially identify diagenetic processes in U-series migration (Eggins *et al.* 2005), although it would appear that it is some time off before reliable error calculations for open system modelling are established (Grün 2006: 14).

Taphonomic considerations suggest that all fossils at Ngandong have been subject to at least some degree of water transport (Grün and Thorne 1997, Westaway 2002, Dennell 2005). Experimental taphonomic studies have indicated that the facial region is the first area to disarticulate during water transport (Boaz and Behrensmeyer 1976; Coard 1999), and the facial regions are missing in all fossil hominins recovered from the Solo river terraces. At least two different layers of sediment have been noted in the vaults of Ngandong *H. erectus*, indicating that at least one redeposition event has occurred (Roberts *et al.* 2005). We can conclude from this that the fossils have been transported and it is possible that material of different age ranges has been accumulated at the site.

When the location of Swisher's excavation is overlain with the original Dutch excavation plans it is apparent that the new specimens acquired through the excavation came from the centre of the area previously excavated in 1932 by the Dutch (Figure 1). The site profile indicates that the original Dutch East Indies Geological survey excavation went down to the marl bedrock, as the excavators had a clear understanding that the hominin remains were situated in the unit directly above the marl (ter Haar 1934), but the fossils used for dating by Swisher *et al.* (1996) were from a post-excavation backfill. The conclusion must be that the dates of Swisher *et al.* (1996) almost certainly do not have any true association with the *Homo erectus* materials.

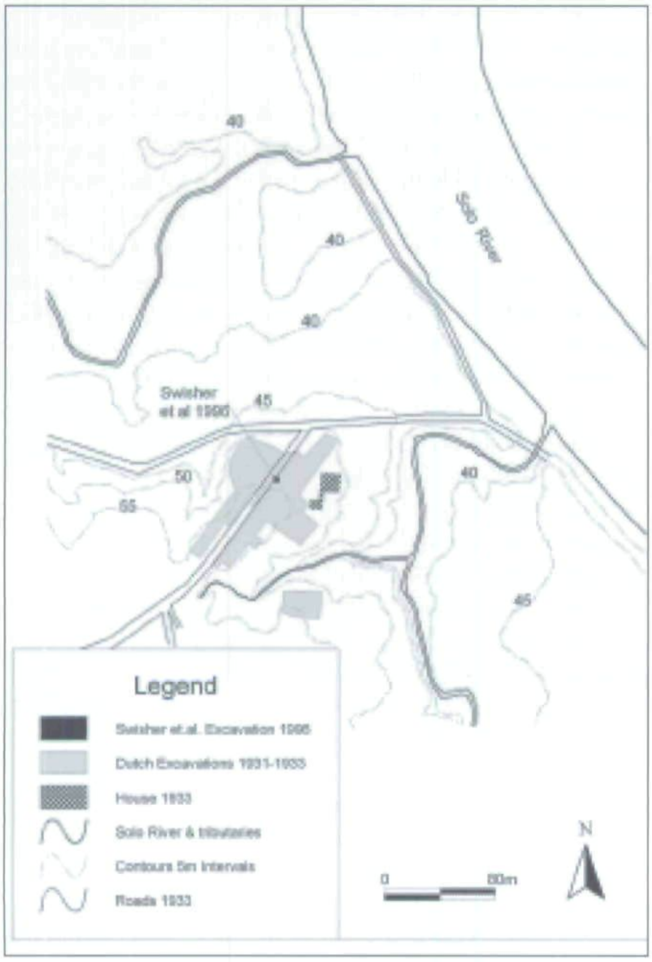

Figure 1. The location of the Swisher *et al.* (1996) excavation in relation to the original Dutch excavations at site 1 (ter Haar 1934).

Testing the phylogenetic case for admixture between *H. erectus* and *H. sapiens*

Support for an assimilation model on chronological grounds is currently contested, but the key question is: did *Homo sapiens* assimilate genes from archaic populations during their migration, and carry to ancient Australia a morphology reflecting this mixed ancestry? Essentially, the argument relies on the presence of a suite of robust cranial traits, which have been considered to be representative of derived traits from Sunda *Homo erectus*.

The Willandra Lakes series, the only Pleistocene series within Australia that has not been reburied, is an important fossil sequence spanning 40,000 years ago to approximately 15,000 years ago. It is crucial to an understanding of whether assimilation is the dominant biogeographical pattern in modern human evolution as suggested by Trinkaus (2005). Could it be the dominant pattern in human evolution within Sunda and Sahul as initially suggested by Curnoe (2007)? An important aspect of the Willandra series is the large range of cranial variation; while the best described individuals are 'gracile', there are a number of very robust crania in the series which have been the focus by Webb (2006) in his most recent discussion on the migration of a *H. erectus* derived population into Australia in the late Pleistocene.

At this point it is important to note that so far we have been discussing cranial robusticity in *Homo sapiens* as if it were a well defined concept; it is not. It is important therefore to determine if there is an identifiable modular pattern of robust expression. Webb (2006: 239-240) defined robusticity in the Willandra series by the following features:

1. Angular cranial vaults, sometimes with a flattened squamae.
2. Thick cranial vault bones.
3. Prominent brow ridges.
4. Rugged muscle attachment areas on the cranium and elsewhere.
5. A pronounced nuchal crest.
6. Large jaws and teeth.
7. Pronounced prognathism.
8. Large, broad faces with rugged malars and prominent zygomatic trigones.
9. Post cranial robusticity including heavily built long bones with thick cortices.

The possession of a combination of these features can therefore be recognised as a module for robusticity.

Methods

Samples of the earliest anatomically modern humans dating between 200-90 ka inside (Omo, Herto, Laetoloi and Jebel Irhoud) and outside of Africa (Skhūl, Qafzeh) and the Australian Willandra series were compared to the *Homo erectus* series from Ngandong.

If the earliest anatomically modern humans had moved through Sunda and assimilated populations of Homo erectus from late sites such as Ngandong, we would presumably see evidence of the combined morphology in the earliest known fossils from Australia. The Willandra series provides the best available case for testing the proposal; it is one of very few modern human skeletal series spanning the period before and during the Last Glacial Maximum outside of Africa. In addition, with the reburial of Kow Swamp, the Willandra series is the only remaining Pleistocene collection of human remains available for analysis. The mark of ancient Java has been identified by a number of workers as being a significant component of the Willandra series (e.g. Hawks *et al.* 2001 and Webb 2006). Tables 1 and 2 provide an overview of the specimens included in the study. Appendix 1 provides an overview of the traits and how they were scored in the phylogenetic analysis.

Willandra Series		
WLH 1	WLH 29	WLH 73
WLH 3	WLH 45	WLH 101
WLH 11	WLH 50	WLH 124
WLH 18	WLH 51	WLH 130
WLH 19	WLH 67	WLH 148
WLH 22	WLH 68	WLH 152
WLH 24	WLH 69	WLH 153
WLH 28	WLH 72	

Table 1. The specimens from the Willandra examined in this study.

Africa	Sunda	The Levant
Omo I	Ngandong V	Skhūl II
Omo II	Ngandong VI	Skhūl V
Bou-VP-16/1	Ngandong VII	Skhūl VI
Bou-VP-16/2	Ngandong X	Skhūl VII
Laetoli 18	Ngandong XI	Skhūl IX
Singa		Qafzeh I
Jebel Irhoud I		Qafzeh III
Jenel Irhoud II		Qafzeh VI
		Qafzeh VII
		Qafzeh IX
		Qafzeh XI

Table 2. Specimens from Sunda, the Levant and Africa examined in this study.

Phylogenetic systematics provides the most logical method for differentiating between individuals of different species. By grading characters and identifying those individuals that share character states we are able to identify specific clades for the different taxa. The primary analytical tool to be incorporated for the cladistic analysis is PAUP Version 4.0 beta, a phylogenetic systematics program that will generate the parsimony analyses for this study.

Another approach to the late Pleistocene hominin record employed in this study is to try to reconstruct the evolutionary history of the various taxa through phylogenetic networks. A phylogenetic network is any network where taxa are represented by nodes and their evolutionary relationships are represented by edges, known as branches in cladistic analysis (Huson and Bryant 2006). Splits networks analyses provide an implicit representation of evolutionary history. Rather than force data into a phylogenetic tree, splits networks explore and visualise the different signals in a data set, while cladistics will select the most parsimonious tree. Splits networks therefore have the advantage of possibly visualising through the internal nodes other kinds of phylogenetic networks, such as recombination, horizontal gene transfer and hybridisation networks (Huson and Bryant 2006). All nodes correspond to hypothetical ancestors. By specifying an outgroup a splits network becomes rooted. This provides more evolutionary meaning as it provides some direction for the network (Huson and Bryant 2006).

The essential aspect to reading the splits network analysis is that the length of an edge in the network is proportional to the weight of the associated split between different taxa. The general relatedness between taxa is defined by the length of the edges; the shorter the path between taxa the more closely they are related to one another. The method suffers in that this distance measurement is quite general, for instance we are not provided with any percentage or frequency assessment. Splits Tree 4 is a recently developed program which is applied in this study to investigate the range of potential phylogenetic networks shared by the fossil series.

Using Webb's criteria, if we present the series in a table to see which specimens are assigned to the robust group and which are considered to be gracile (Table 3), WLH 18, 19, 27, 28, 45, 50, 69, 73, 100, 101 and 154 have a number of features, while WLH 16, 22, 63, 107 and 110 have only one or two robust traits (Webb 2006: 239). Pardoe (2006) has argued that the variation can be explained more appropriately by sexual dimorphism; amongst the robust individuals, only WLH 45, 73 and 100 have been identified as female, while WLH 16 and 63 are of undetermined sex, the remaining 11 being male (Webb 1989).

As can be seen from Table 3, there are very few individuals in the series where a suite of these characters can be investigated in their entirety; the collection is quite fragmentary. Using Webb's criteria, it also becomes apparent that a number of the individuals do not demonstrate a typically robust or gracile morphology, but share a combination of Webb's defining traits. Certainly there are a number of individuals within the series of 26 that do score only robust features, namely WLH 18, 19, 28, 50, 69, 124, 148, 152 and 154, all of which with the exception of WLH 154 (which Webb has not studied) are designated as males (Webb 1989, 2006). A number of individuals share a combination of robust and gracile characters; the distinction between robusts and graciles is not very clear. Although there are 8 individuals with mixed characters, 9 would appear to be quite consistently robust, and 9 appear to be quite consistently gracile. Brown (2000) and Pardoe (1991, 2006) argued that the variation evident in the Willandra series can be explained by the differences between sexes: the majority of the fossil crania identified as male are heavily built, while the more gracile individuals are female (Pardoe 1991). Although robusticity would appear to be closely associated with sexual dimorphism, there is an interesting pattern amongst the dated fossils suggesting that it also correlates with the approach of greater aridity and the LGM (4 of the robust crania have been reliably dated and all sit around the LGM). Oppenheimer (2004) suggested that the appearance of robusticity later in the Pleistocene may in fact represent a later migration into Australia of people along the southern route to Australia who had assimilated a Ngandong-like population. Needless to say there are still many questions to be answered in relation to the nature of cranial robusticity at the Willandra Lakes and it is a worthy endeavour to assess the possibility of admixture.

Specimen number	1. AV	2. TCV	3. PBR	4. RMA	5. PNC	6.LJT	7.Prog	8. LF & M	9.PC robust
WLH 1	0	0	0	0	0	-	-	-	-
WLH 3	0	0	0	0	0	+	+		+
WLH 9	-	0	-	-	-	-	-	-	0
WLH 11	0	0	-	-	0	0	-	0	0
WLH 18	-	+	+	-	-	-	-	-	+
WLH 19	+	+	+	+	+	-	-	-	-
WLH 22	0	+	-	0	0	+	-	-	0
WLH 24	0	0	0	0	-	-	-	-	0
WLH 28	+	+	-	+	+	-	-	-	+
WLH 29	0	0	-	0	-	-	-	-	-
WLH 45	+	+	0	0	-	-	-	-	+
WLH 50	+	+	+	+	+	-	-	+	+
WLH 51	-	0	0	-	-	-	-	-	-
WLH 52	-	0	-	-	0	-	-	-	-
WLH 68	-	0	0	-	-	-	-	-	-
WLH 67	0	0	0	+/0	+	-	-	0	+
WLH 69	-	+	+	+	-	-	-	-	+
WLH 72	+	+	0	+	+	0	-	-	0
WLH 73	0	0	+	0	-	-	-	-	-
WLH 101	-	+	+	-	-	-	-	-	-
WLH 124	-	+	+	-	-	+	-	-	+
WLH 130	0	0	0	0	+	-	-	-	-
WLH 143	-	0	-	-	-	-	-	-	-
WLH 148	+	+	-	+	+	-	+	+	+
WLH 152	+	+	+	+	-	+	-	+	+
WLH 154	-	-	+	-	-	+	+	-	-

Table 3. Robust and gracile traits in the Willandra fossil human series are scored according to Webb's criteria: + = robust, 0 = gracile, +/0 = intermediate, - = missing value.

Results

The bootstrap analysis provides a very crude summary of hierarchical clustering within the 45 operational taxonomic units (OTUs) (Figure 2). Resolution of clades between the specimens employed in this cladistic analysis is understandably not very illuminating as the time frame is largely restricted to hominins within the last 200,000 years of human evolution. While it has no success in differentiating between *Homo sapiens* and the early African taxa, such as Ndutu and Olduvai Hominid 9, it does clearly delineate between the ingroup taxa and the Ngandong series. The cladistic analysis essentially reveals that the two species are separate clades. The internodes leading to Ngandong indicate that it is a terminal taxon with no relative relationship to the Willandra specimens. With KNM-ER 3733 (now accepted by most as *Homo ergaster*) placed as the outgroup in the cladogram Ngandong is clearly identified in the analysis as a sister taxa to the *H. sapiens* group and is not ancestral to any of the Willandra OTU's.

In the neighbour joining analysis featured in Figure 3 there is greater separation of OTU's. The Ngandong series once again clusters from the remaining OTUs forming a distinct network. The nearest neighbours are OH 9 and Omo II. The branch length between the Willandra and Ngandong specimens is significant. It illustrates no ancestor-descendant relationship between the two clades; they are on separate evolutionary trajectories. The relative relationship

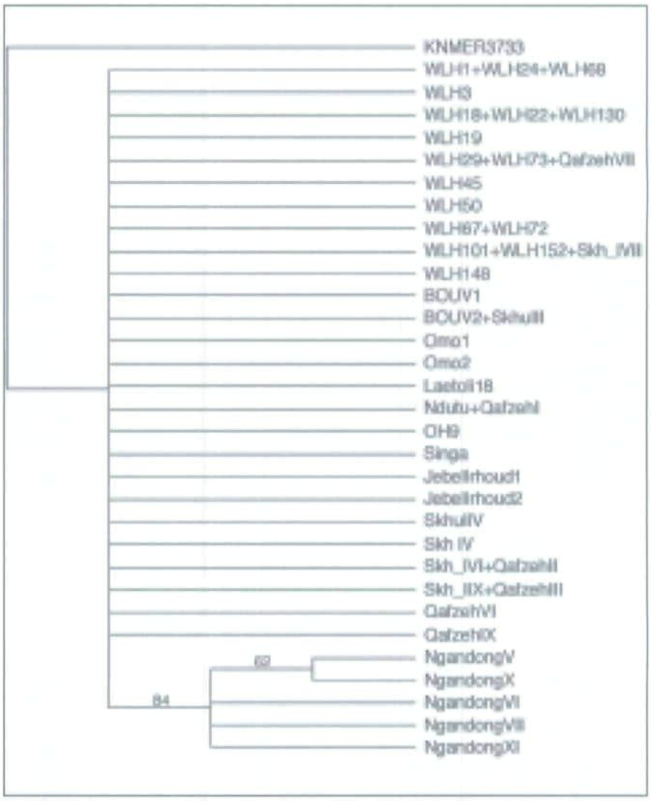

Figure 2. Cladistic bootstrap analysis incorporating 45 individual fossil specimens.

between the various OTUs clearly distinguishes Ngandong from the Willandra series.

Splits tree does provide an opportunity to begin exploring the possibility of hybridisation events between species. The splits tree in Figure 4 contains a number of internal nodes that represent lineages of descent and perhaps even reticulate events, such as hybridization, horizontal gene transfer or recombination. The corresponding branch length represents the distance of separation between the taxa, that is to say, the greater the branch length, the greater the split length. The distribution of early *Homo sapiens* across the splits network demonstrates their large cranial variability. The Willandra series is linked with this network and would seem to reflect the huge range of variation within this series. The five OTUs from Ngandong cluster in a network away from the majority of *Homo sapiens* with the exception of Omo 2 and OH9. Four other OTU's, namely Skhūl V and VI and Jebel Irhoud I and II, also very loosely group with the network of early archaic *sapiens* and the Ngandong series, although the branch length between the early *sapiens* is considerable and they can be clearly distinguished from the Ngandong OTUs.

In Figure 5 an outgroup has been identified, KNMER 3733. As in Figure 4, the Ngandong network in the rooted splits network is clearly distinguished from the Willandra network and indicates that the phylogenetic relationship between the two series is not close. The purported link between robust Australian specimens and the Ngandong series is not supported in the split network. The Ngandong series demonstrates a considerable split from the Willandra series.

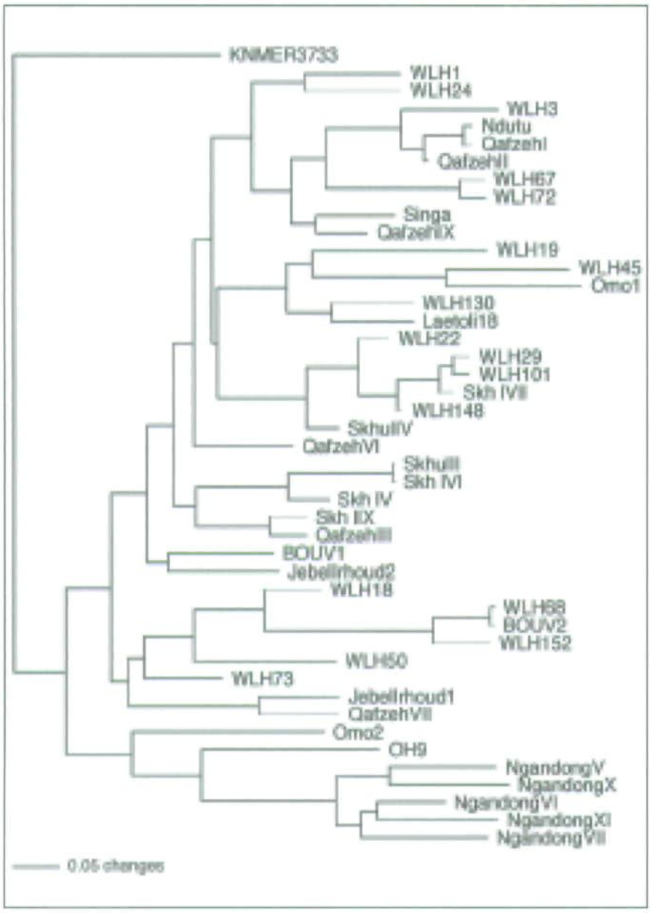

Figure 3. Neighbour joining analysis incorporating 45 individual fossil specimens.

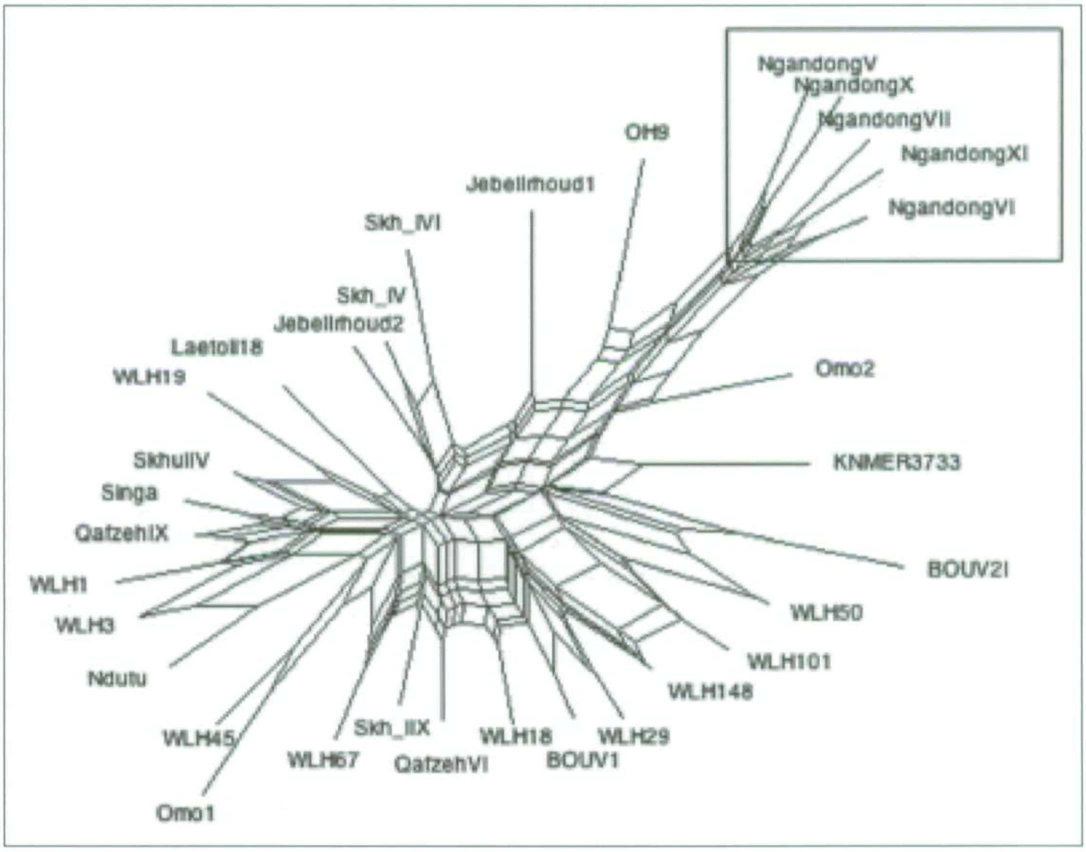

Figure 4. Unrooted splits tree of data matrix incorporating 45 individual taxa.

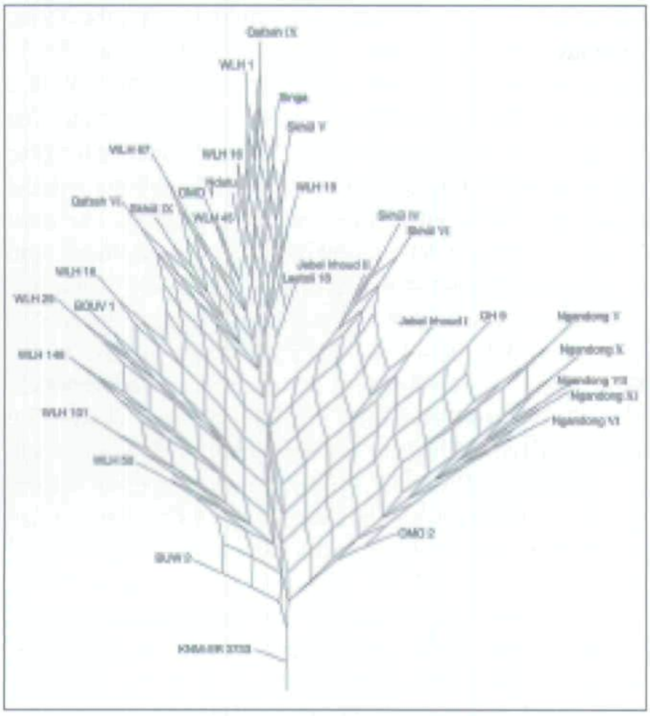

Figure 5. A rooted splits tree of the 45 specimens.

Discussion

The legacy of Weidenreich has seen an exhaustive treatment and review of the question of *Homo erectus* input into the peopling of Ancient Australia. The past few decades has seen the Multi-regionalist position shift from linear evolution in the region (Weidenreich 1946, Coon 1962), to genetic exchange between archaic populations in the maintenance of regional specific traits (Thorne and Wolpoff 1981), to a model that largely incorporates assimilation of archaic populations by modern humans (Curnoe 2007). None of these hypotheses has found much support in either the archaeological or human palaeontological record when closely scrutinized (e.g. Larnach and Macintosh 1974, Macintosh and Larnach 1976, Brown 1981, Groves 1989, Habgood 1989, Brown 1992, Storm 2001, Cameron and Groves 2004, Durband 2007, Kaifu *et al.* 2008). It would appear that a process of species replacement is the dominant human evolutionary pattern in Sunda.

It is very possible that a process of species replacement without any significant hybridisation was a long term evolutionary pattern in Sundaland. The earliest hominins in Java from the site of Sangiran demonstrate a higher range of variability than among later *Homo erectus* (Kaifu *et al.* 2005), and an important question still seems to be whether some of the earliest specimens actually constitute a different species from *Homo erectus*. The debate on the possible presence of more than one species in Java has a long and complex history (e.g. Robinson 1953, Howell 1961, Robinson 1962, Tobias and von Koenigswald 1964, Twiesselmann 1973, Krantz 1975, 1994, Orban-Segebarth and Procureur 1983, Franzen 1985, Tyley 1994, Kramer 1994). Is it possible that these early fossil fragments sit more comfortably in a grade of hominisation equivalent to that of an earlier hominin, such as *Homo habilis*? Certainly the discovery of *Homo floresiensis* provides suggestive evidence that a pre-*erectus* hominin had migrated into the region (Argue *et al.* 2006). The early dates for Modjokerto (Huffman 2001, Morwood *et al.* 2003) provide further tantalising evidence for a potential pre-erectine species on Java, as we do not really know what the infant calotte represents.

If, on the other hand, all early fossils from Java do represent *Homo erectus*, then in the Early Pleistocene it must have been a morphologically diverse species, and some evolutionary event, perhaps resulting in a genetic bottleneck, might explain the reduction in morphological diversity. One possible such event is the Australasian strewnfield, a meteorite event which has been documented as having catastrophic impacts at Sangiran, initiating such activities as increased volcanism and tectonic movement (Brasseur et al 2007). *Homo erectus* cranial morphology, as we know it from Sangiran 17 and others from the unit above the Grenzbank, maintained a separate identity for a long period of time, and it would appear from the available evidence in the fossil record that there was little external influence in the genotype.

If another earlier species of human lived in Sunda before the arrival of *H. erectus* then the extinction of *H. erectus* is likely to simply represent the latest extinction in a pattern of replacement within the region, following the movement of *H. sapiens* into it.

This picture is complicated as the evidence to suggest that *H. erectus* and *H. sapiens* overlapped for any amount of time in Java still waits to be discovered. Future excavations at Ngandong may identify an overlap but currently the only reliable evidence is further to the east in Flores where a very different species, predating *erectus*, likely survived in a very different habitat. *Homo floresiensis* seems to have been contemporary with modern humans in eastern Indonesia, even if modern people were not yet on Flores itself, for perhaps as long as 40,000 years. The results of a dating program at Punung indicate that the age of the cave sites are perhaps greater than 120 ka (K. Westaway *et al.* 2006). As Ngandong consists of a more archaic fauna than Punung, which is essentially a modern fauna (e.g. Punung has modern forms of elephants while Ngandong has *Stegodon*) it would suggest that the site of Ngandong has an age range at least greater than 120 ka.

If there is no evidence of significant temporal overlap between *H. erectus* and *H. sapiens* in the archaeological record of Java do we see such evidence in the form of assimilation? The answer again is no; the cladistics analysis (in particular the bootstrap analysis) has identified Ngandong as a sister taxa to the *H. sapiens* series with a shared common ancestor in the earlier *Homo ergaster* specimen KNM ER-3733. The splits network analysis provides a complementary result and has identified a considerable split between the Willandra series and the Ngandong specimens incorporated in this analysis. The results of the splits network analysis identifies no close network through branching between the Willandra series and *Homo erectus* from Ngandong. If there was an ancestor and descendant relationship, or one that indicated hybridisation between the two series, we would expect to see a shared network. Of particular interest is the fact that none of the robust Willandra crania (which are the individuals that according to Curnoe's 2007 paper would represent the fossils necessary to support a model of hybridisation) share branches with the Ngandong series. WLH 50, described by a number of workers as closely aligned to Ngandong is in fact positioned on the opposite branch of the splits network, indicating a considerable biological distance between the two taxa. Similarly WLH 19 is closely aligned with robust specimens of *Homo sapiens* such as Laetoli Hominid 18, but is not closely aligned with the Ngandong cluster.

OH 9, around which there seems to be some taxonomic confusion (Cameron and Groves 2004) and Omo II, considered by some to be an archaic *Homo sapiens* (Schwartz and Tattersall 2003), are the only two that cluster in some proximity with the Ngandong network. As OH 9 is considered by many to be a *Homo ergaster* (once known as African *H. erectus*) it makes sense that it would be placed in phylogenetic terms much closer to the Ngandong network. Like KNM ER-3733, OH 9 is perhaps ancestral to the Ngandong individuals.

In sum, none of the OTU's identified in this analysis present themselves as contenders for a hypothetical hybrid between the two species. As noted by others (e.g. Kaifu *et al.* 2008) *H. erectus* has likely been on a separate evolutionary trajectory from *H. sapiens* for a considerable period, and the evidence presented here indicates that this evolutionary event on the periphery of the human range contributed little or nothing to the ancestry of modern humans arriving into Sahul.

While splits network analysis is effective as a means of visualising potential phylogenetic signals between archaic and modern populations it does not provide a means to effectively measure the actual biological distance as a percentage or through frequency assessment. It is hoped that future developments within the technique will enable distance measurement to be more quantifiable rather than simply provide a general measurement through branch length.

Much has been made of the range of morphological variability within the Willandra Lakes series. The Willandra series is important for understanding Australian origins as it dates to the period from soon after initial colonisation until the protracted event known as the Last Glacial Maximum. The range of variation in the series is, however, not unique. A great range of variation can also be seen in the only other fossil series of modern humans outside of Africa and dating to the period before the Last Glacial Maximum, i.e. from the Levant, mainly from Skhūl and Qafzeh.

An interesting hypothesis raised by the Willandra series is the possible correlation of cranial robusticity with the Last Glacial Maximum. The LGM has been considered by a number of researchers as a possible mechanism that selected for a more robust cranial morphology (Wright 1976, Bulbeck 2001, Stone and Cupper 2003, Westaway 2006). Important here is the fact that the first Australians, WLH 1 and WLH 3, are gracile and preserve none of the traits that we see in late *H. erectus*. Nor is there any evidence for later migrations involving populations incorporating assimilated traits from *H. erectus* (and hence explaining the later appearance of a robust morphology). Like the Skhūl and Qafzeh series, the Aboriginal cranial morphology from the Willandra Lakes Region expresses considerable diversity in a single population. Over the 25,000 year period of the Willandra sequence, a period in which there were dramatic climatic fluctuations, the region became semi-arid, somewhat similar to the environments of Mongolia and Tierra del Fuego (Bowler 1998). A modern tropical hunter-gatherer coloniser population over many thousands of years adapted to the harsh conditions of the Last Glacial Maximum.

If we are to assess if a correlation exists between glacial conditions and cranial robusticity the next step must be improving the chronologies for the Willandra series to determine if the correlation is a true phenomenon. Devising techniques to understand how dramatic environmental change and other external stimuli might select for greater robusticity are currently the focus of much international research and have the potential to shed further light on explaining phenotypic expression within late Pleistocene Australia. While the mark of Ancient Java may not be present in any of the fossil series from the Willandra, establishing a clearer understanding of the micro-evolutionary processes that may have produced variation in Pleistocene Aboriginal Australians has the potential to inform the international community of the influence the extreme conditions of the Quaternary may have had on modern human morphology and diversity.

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