

John Hawks

Department of Anthropology,
University of Utah,
Salt Lake City, UT 84112,
U.S.A. E-mail:
john.hawks@anthro.utah.edu

Stephen Oh

Paleoanthropology Laboratory,
Department of Anthropology,
University of Michigan,
Ann Arbor, MI 48109-1382,
U.S.A.

Keith Hunley

Paleoanthropology Laboratory,
Department of Anthropology,
University of Michigan,
Ann Arbor, MI 48109-1382,
U.S.A. E-mail:
khunley@umich.edu

Seth Dobson

Department of Anthropology,
Washington University,
St. Louis, MO 63130,
U.S.A. E-mail:
sddobson@artsci.wustl.edu

Graciela Cabana

Paleoanthropology Laboratory,
Department of Anthropology,
University of Michigan,
Ann Arbor, MI 48109-1382,
U.S.A. E-mail:
graciela@umich.edu

Praveen Dayalu

Paleoanthropology Laboratory,
Department of Anthropology,
University of Michigan,
Ann Arbor, MI 48109-1382,
U.S.A.

Milford H. Wolpoff

Paleoanthropology Laboratory,
Department of Anthropology,
University of Michigan,
Ann Arbor, MI 48109-1382,
U.S.A. E-mail:
wolpoff@umich.edu

An Australasian test of the recent African origin theory using the WLH-50 calvarium

This analysis investigates the ancestry of a single modern human specimen from Australia, WLH-50 (Thorne *et al.*, in preparation; Webb, 1989). Evaluating its ancestry is important to our understanding of modern human origins in Australasia because the prevailing models of human origins make different predictions for the ancestry of this specimen, and others like it. Some authors believe in the validity of a complete replacement theory and propose that modern humans in Australasia descended solely from earlier modern human populations found in Late Pleistocene Africa and the Levant. These ancestral modern populations are believed to have completely replaced other archaic human populations, including the Ngandong hominids of Indonesia. According to this recent African origin theory, the archaic humans from Indonesia are classified as *Homo erectus*, a different evolutionary species that could not have contributed to the ancestry of modern Australasians. Therefore this theory of complete replacement makes clear predictions concerning the ancestry of the specimen WLH-50. We tested these predictions using two methods: a discriminant analysis of metric data for three samples that are potential ancestors of WLH-50 (Ngandong, Late Pleistocene Africans, Levant hominids from Skhul and Qafzeh) and a pairwise difference analysis of nonmetric data for individuals within these samples. The results of these procedures provide an unambiguous refutation of a model of complete replacement within this region, and indicate that the Ngandong hominids or a population like them may have contributed significantly to the ancestry of WLH-50. We therefore contend that Ngandong hominids should be classified within the evolutionary species, *Homo sapiens*. The Multiregional model of human evolution has the expectation that Australasian ancestry is in all three of the potentially ancestral groups and best explains modern Australasian origins.

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Introduction

Since its discovery in 1982, Willandra Lakes Hominid (WLH) 50, as reconstructed by A. Thorne, has figured prominently in discussions of modern human origins in Australia and Indonesia (Thorne, 1984; Webb, 1989; Thorne & Wolpoff, 1992; Frayer *et al.*, 1993, 1994; Stringer, 1998). Dated to some 15–13 ka by gamma spectrometric *U*-series analysis (Simpson & Grün, 1998), and to about double that by ESR (on bone, by Caddie *et al.*, 1987), the WLH-50 calvarium appears on inspection to exhibit many features that closely resemble earlier Indonesian hominids, including the Ngandong fossils of Java [Thorne, cited in Wong (1999); Thorne *et al.*, in preparation; Wolpoff, 1999]. Those authors who support a multiregional model of human evolution view the similarities between the Ngandong hominids and WLH-50 as phylogenetic, meaning in this case that these specimens are members of the same evolutionary species and share some features by virtue of having come from the same region of the world (Frayer *et al.*, 1993, 1994). Ngandong is one of the probable ancestors of WLH-50, in this view,¹ or the two may share a recent common ancestor. However, authors who support the recent African replacement

hypothesis of modern human origins in Australasia have explained the seemingly archaic nature of WLH-50 differently, as a consequence of either its size and related robusticity or possibly pathology (Stringer, 1998; Webb, 1990), but not as a result of any significant ancestor–descendant relationship with earlier Australasian populations. *Despite these differences, both interpretations agree on one fundamental item; WLH-50 is a modern human* (Thorne, 1984; Wolpoff, 1989, 1999; Stringer, 1998).

We therefore begin with the supposition that earlier Late Pleistocene Africans, Levantines (Near Eastern individuals from Skhul and Qafzeh), and WLH-50 are members of the same species, *Homo sapiens*, and all represent modern humans or their immediate ancestors. There are two different predictions about the pattern of ancestry, and it is from these that we can develop a test for the African replacement model for modern human origins. The replacement model asserts:

- (1) The earlier Late Pleistocene Africans and Levantines are likely to be direct ancestors of WLH-50 by virtue of age and geography.
- (2) The Ngandong hominids cannot be direct ancestors of WLH-50, by virtue of being in a different species, *H. erectus* (Rightmire, 1990), whose habitation on Java may have persisted well into the late Pleistocene (Swisher *et al.*, 1996).

¹Even if the most recent Ngandong date estimate is correct (Swisher *et al.*, 1996), and the oldest WLH-50 estimate is correct (Caddie *et al.*, 1987), Ngandong is older than WLH-50, and the Indonesian site may be considerably older (Grün & Thorne, 1997).

The complete replacement hypothesis requires that there is a unique relationship between early modern humans, represented by the earlier Late Pleistocene Africans, Levantines, and WLH-50, to the exclusion of more archaic hominids from Ngandong.

We propose to test this complete replacement hypothesis by demonstrating that one or both of the above assertions must be incorrect. A recent African replacement explanation of modern human origins in Australasia is incorrect if it could be shown in a comparison of WLH-50 to earlier Late Pleistocene Africans, Levantines, and the Ngandong people that the closest relationships are to Ngandong. This is because complete replacement predicts unique relationships between WLH-50 and the late Pleistocene Africans and individuals from Skhul/Qafzeh to the exclusion of Ngandong. Multiregional evolution, in contrast, views all three of these groups as potential ancestors for WLH-50.

We have chosen two procedures to examine the relationship of WLH-50 to the African, Levantine, and Indonesian samples:

- (1) A discriminant analysis of metric data which differentiates the Africans, Levantine, and Ngandong hominids into three groups and can be used to assess the group affinity of WLH-50, and
- (2) a pairwise difference analysis using non-metric data, comparing WLH-50 with the individuals in these three samples.

The prediction of the replacement model is that WLH-50 will sort with the Africans or Levantines in both tests, since it must be uniquely descended from these groups. If these procedures find that WLH-50 clusters with Ngandong rather than with Africans or Levantines, then it must follow that WLH-50 shares no special relationship with Late Pleistocene hominids from Africa and the Levant that would exclude the

Table 1 Specimens in the comparative samples

Ngandong	Late Pleistocene Africans	Levantines
1	Jebel Irhoud 1	Skhul 5
4*	Jebel Irhoud 2	Skhul 9
5	Laetoli 18	Qafzeh 6
6	Omo 1*	Qafzeh 9
9	Omo 2	
10	Singa	
11		

*Used only in the nonmetric analysis.

Ngandong hominids from its ancestry. In this case, replacement would be refuted as a model for the ancestry of Australasia, and the Ngandong hominids must be accepted as *H. sapiens*.

Materials and methods

Our fossil sample consists of the possible Pleistocene ancestors for WLH-50 from the Levant, Africa and Indonesia, as described above. Seventeen crania from the earlier part of the Late Pleistocene were chosen for comparison with WLH-50 (Table 1). We assigned all fossils except for WLH-50 to one of three groups based on geography. These are the most complete crania from this time period in these regions and include the specimens that preserve all or most of the areas that are observable on WLH-50. Fragmentary specimens and specimens too recent to be potential ancestors of WLH-50 were excluded from this study. The metric variables were chosen to maximize the number of measurements we could replicate in all the crania. The incomplete condition of WLH-50 limited us to 21 variables, mostly standardized chords and arcs, which could be accurately and repeatedly measured. All of them were present on all crania, and no missing data were allowed for the discriminant analysis.

Four measurements of WLH-50 required a reconstruction of the glabella region,

Table 2 Comparison of selected measurements by different authors* for WLH-50

WLH-50 Measurement (in mm)	Stringer (1998) value	Brown (1998) value	This study
Biasterionic breadth	123	127	123
Biauricular breadth	138		138
Biparietal breadth	142	139	142
Bregma-asterion	151	151	150
Bregma-lambda	127	130	129
Thickness at bregma		17	17
Central parietal thickness		14	16
Cranial length	211	212	212
Maximum cranial breadth		151	150
Maximum frontal breadth	117		124

*The comparisons are limited to measurements published by these authors and do not include the full set of 21 measurements used for analysis in this paper.

which was accomplished by molding clay to follow the existing supraorbital contour seen in superior and facial views. It was assumed that there was no depression at glabella. Few later Pleistocene Australians (e.g., Kow Swamp and Coobool Creek samples) have a glabellar depression. Therefore all measurements involving glabella represent maximum values. The measurements (Table 2) are consistent with measurements published by Stringer (1998) and Brown (1998).² For example, our cranial length, which includes the reconstructed glabella, is 212.2 mm while Stringer's value is 211.0 mm and Brown's is 212 mm. Most of the other comparisons are quite close; only one of the measurements we present is significantly

²This reference is a web page and differs somewhat from a regular journal reference (Poumay, 1998), not only because there has been no peer review of its content, but also since a web page can be modified at any time without record of the changes. For instance, the address of the Brown web page we cite here, and some of its content, changed between submitting this paper in 1998 and reviewing the final manuscript in 1999. Stringer (1998) quotes from the 1998 site in support of his analysis and assumptions, and we address here some of the issues raised in the web site text as well as reproduce a view of the WLH-50 vault from the cite, with Brown's permission. As it happens, no substantial differences in the points discussed occur on the 1999 site, but this may not be true in the future.

different from Stringer's, as addressed below.

All other measurements of fossil crania were taken on the original specimens by one of us (MHW), with a small number of exceptions. A combination of published and cast measurements were used for Laetoli Hominid 18 (Magori & Day, 1983), and Omo 2 (Day & Stringer, 1991). We checked both for the accuracy of casts in the Paleo-anthropology Laboratory at the University of Michigan and at the National Museums of Kenya, and for equivalent measurement definitions with all published sources.

The nonmetric observations on the comparative samples (see Table 4) were made by pairs of observers on casts. We used only variables that could be unambiguously and repeatedly scored on the high quality replicas available to us. Our 16 nonmetric traits represent an exhaustive list of all characteristics that could be scored on WLH-50. We avoided duplicating features that seemed to reflect the consequences of the same anatomical variation. The work was done on consecutive days to insure the same criteria were applied to all specimens. In our scoring system, the presence of a trait was scored as a one (1), and absence as zero. Some of these traits may reflect robustness, and for all such traits the more robust condition was scored as one.

Discriminant function analysis

Our first approach emphasized the ability of metric data to discriminate the members of geographic groups. Discriminant function analysis allows the investigators to examine or predict group membership for samples of unknown group affinities by using multiple variables taken for a set of cases with known group affinities. It is a robust technique whose use is most valid when the specimen to be discriminated is a member of one of the groups defining the function. Discriminant functions are commonly used for

Table 3(a) Unstandardized discriminant function coefficients for the five variables chosen in the stepwise function to separate the three groups

Variable (mm)	Discriminant function 1	Discriminant function 2
Cranial length	0.396	- 0.075
Glabella-bregma	0.318	0.207
Bregma-asterion arc	- 0.721	0.021
Central parietal thickness	0.988	0.190
Medial supraorbital height (Constant)	- 0.508	0.039
	2.368	- 13.541

Calculations are based on the Wilks' Lambda statistic, and the functions are normalized around the origin. These values reflect the absolute importance of the independent variables in contributing to discrimination. See Figure 2 for the results.

Table 3(b) Standardized discriminant function coefficients

Measurement	Function 1	Function 2
Maximum cranial length	3.437	- 0.649
Medial supraorbital height	- 1.512	0.117
Central parietal thickness	2.416	0.464
Glabella-bregma	1.600	1.042
Bregma-asterion arc	- 4.631	0.137

These values reflect the relative importance of the independent variables in contributing to discrimination.

identification in forensic anthropology (e.g., Gill & Rhine, 1990).

We reasoned that if we could determine a discriminant function that accurately distinguished the three groups, it could be validly applied to WLH-50 because each group is a potential ancestor of this specimen. With regard to these samples, the competing modern human origins hypotheses for Australasia disagree only about the potential of a Ngandong ancestry, which the replacement hypothesis holds to be zero. The discriminant function we calculated is uniquely determined to distinguish the three groups on the basis of measurements known for all of their members. Therefore, the expectation of the replacement hypothesis is that WLH-50 should sort with either the

Table 3(c) Total structure coefficients for all independent variables

Measurement	Function 1	Function 2
Maximum cranial length*	0.245041	0.137516
Medial supraorbital torus height*	0.165216	0.052964
Bregma-asterion arc*	- 0.82218	0.38818
Glabella-bregma*	0.147245	0.825686
Central parietal thickness*	0.333043	0.533806
Glabella-inion	0.271686	0.230179
Glabella-lambda	- 0.1479	0.201619
Bisupramastoid breadth	0.739836	0.122409
Biparietal breadth	0.237524	0.267109
Biasterionic breadth	0.626238	0.168729
Minimum frontal breadth	0.39857	- 0.12133
Bifrontotemporale breadth	- 0.06242	0.084195
Maximum frontal breadth	0.152752	0.265026
Nuchal torus height	0.482174	- 0.1689
Lateral supraorbital torus height	0.557043	- 0.11858
Central supraorbital torus height	0.190555	0.427552
Lambda-inion	- 0.35891	0.018806
Lambda-asterion	- 0.72614	- 0.07127
Inion-asterion	0.600948	- 0.0112
Bregma-lambda	- 0.6142	- 0.19288
Bregma-asterion	- 0.59628	0.245766

These indicate the correlations of each independent variable to the discriminant functions.

*Included in discriminant functions.

Africans or Levantines, since only these two groups may contain the ancestors of this specimen. If replacement is true, WLH-50 should not sort with the Indonesians.

We began by finding whether a function could be calculated from our set of 21 measurements that would accurately and unambiguously distinguish the three comparative samples. Using SPSS version 8.0, we calculated a stepwise discriminant function using the Wilkes-Lambda statistic. The advantage of this commonly used test statistic is that at each step it maximizes the cohesiveness within each group without affecting the separation between groups (Klecka, 1980). Our discriminant analysis employed the 21 metric variables [Table 3(c)] that could be found on the 15 fossil crania, which are in three groups (Table 1).

A stepwise function, as we used, examines the relationships of all the metric variables to group memberships and chooses those variables that are best able to discriminate the groups. The function that was calculated [Table 3(a)] correctly classified every member of the three groups using five measurements. These classifications of known specimens were without exception robust to crossvalidation using the other known specimens, confirming the utility of this set of measurements for determining geographic origin.

We then applied the function to WLH-50. Because this discriminant analysis is based on the geographic associations of fossils, in groups that are potentially ancestral to WLH-50, it provides a test of the replacement hypothesis with little Type 1 error. If WLH-50 discriminates with an Indonesian sample, and not with an African or Near Eastern sample, then it provides a strong refutation of the replacement hypothesis. We do not contend that this procedure provides a means of estimating the proportion of relationship among WLH-50 and the three comparative groups—it certainly does not. However, even given the small sample sizes available for this analysis, it would be very surprising for WLH-50 to be classified with the Indonesian sample if the replacement hypothesis were true.

Pairwise difference analysis

If our first approach emphasized discrimination, our second emphasized cohesiveness. We addressed the relationship of individuals in a way that ignored group assignments, to determine if there were patterns of features that could link specimens to their geographic origins. For this, we calculated the pairwise differences between WLH-50 and the 17 other specimens (Table 1) using non-metric traits (Table 4). We were able to include more individuals in this analysis because it is tolerant of missing data, as long as the missing data are randomly distributed

as is true for these groups of specimens (Kruskal–Wallis test, chi square=0.126, $P=0.939$). In cases where a trait could not be scored on a specimen, we scored the trait as missing for that individual, and treated it as no difference in all comparisons involving that individual.

Of the 16 nonmetric variables used in the final analysis, six were correlated with cranial capacity (Kolmogorov–Smirnov test), which provides a proxy for cranial size that is not based on any of the measurements in our analysis. In each instance where the presence of a nonmetric feature was correlated with cranial capacity, the specimens that possessed the feature had smaller cranial capacities than those that lacked the feature. For example, specimens that possessed a mastoid crest were more likely to have smaller cranial capacities than those that lacked this feature. These relations are no doubt due to the fact that Ngandong is the most robust segment of our sample, and has the smallest mean cranial capacity. However, this association did not hold within groups. There were no significant within-group associations of cranial size and presence of nonmetric traits in our samples (Africans: $P=0.527$; Levantines: $P=0.901$; Ngandong: $P=0.580$; Mann–Whitney test). Comparing the African and Levantine samples alone, there is a positive correlation, indicating that any correlation between cranial size and presence of non-metric features must depend strongly on the geographic locations of the groups being compared (Figure 1). These non-metric trait comparisons should therefore be excellent indicators of geographic affinities among these samples.

Pairwise difference analysis is commonly applied to DNA sequence data to derive information about past population demography (Rogers, 1995). It has also been applied to sequence data to investigate the closeness of relationship that a single ancient individual has to samples of living humans from

Table 4 Nonmetric features

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1. **Transversely extensive nuchal torus**—This feature is scored as present (1) if a distinct nuchal torus defined by superior and supreme nuchal lines extends transversely across the entire occipital bone.
 2. **Sulcus dividing the medial and lateral elements of the supraorbital torus/superciliary arches**—This feature is scored as present (1) if a clear sulcus can be identified that divides the supraorbital torus or superciliary arches, whatever the case may be, into medial and lateral elements.
 3. **Frontal sagittal keel**—A thickening along the midline of the frontal bone anterior to bregma. The feature is scored as present (1) if it can be visually and tacitly identified. It need not extend along the entire length of the frontal bone.
 4. **Parietal sagittal keel**—A thickening along the sagittal suture. This feature is scored as present (1) as long as it can be identified anywhere along the suture.
 5. **Superior margin of the orbit**—Scored as either blunt (1) or sharp (0). If the margin is blunt then the supraorbital surface grades evenly into the inferior surface of the frontal bone.
 6. **Supraorbital fossa**—An elliptic depression on the occiput above the superior nuchal line. Scored as present (1) or absent (0).
 7. **Temporal line forms a ridge**—This feature is scored as present (1) if the temporal lines form a ridge along the frontal bone, posterior to the post-orbital constriction.
 8. **Projectinginion**—This feature is scored as present (1) if the nuchal torus/line projects posteriorly at the most inferior midline point along the superior nuchal lines.
 9. **Pre-bregmatic eminence**—This feature is scored as present (1) if a distinct eminence can be visually identified anterior to bregma when viewing the specimen in Frankfurt Horizontal. If the frontal bone and the parietals form an even curve in Frankfurt Horizontal then the feature is scored as absent (0).
 10. **Angular torus**—This feature is scored as present (1) if the posterior temporalis muscle attachment forms a raised and thickened ridge at its furthest backward extent.
 11. **Post-lambdoidal eminence**—This feature is scored as present (1) if a distinct posteriorly projecting eminence can be visually identified immediately posterior to lambda when viewed in Frankfurt Horizontal. The scores for this feature are the same as those for the “raised lambdoidal suture” [Brown \(1998\)](#) mentions on his web page, and we believe the different observations record fundamentally the same feature.
 12. **Linea obliquus**—This feature is scored as strongly developed (1) if there is a clear line or ridge extending inferiorly and anteriorly from the lateral portion of the nuchal line/torus.
 13. **Lateral frontal trigone**—A backward-facing triangular development at the lateral-most portion of the supraorbital torus (see [Figure 6](#)). The apex is created when a prominent temporal ridge meets a clear line on the anterior portion of the supraorbital torus.
 14. **Mastoid crest**—This feature is scored as present (1) if a distinct bony crest can be identified that extends inferiorly and slightly anteriorly from the top of the mastoid process towards the tip of the mastoid process.
 15. **Supramastoid crest**—This feature is scored as present (1) if a distinct bony crest can be identified that curves posteriorly and slightly superiorly from the root of the zygomatic arch on the temporal bone above the mastoid process.
 16. **Coronal keel**—A thickening of raised bone extending transversely from bregma along the coronal suture.
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different regions of the world ([Krings et al., 1997](#)). In these genetic analyses, the number of nucleotide differences between all possible pairs of individual DNA sequences are

counted, and the results are presented as the frequency distribution of the number of differences. The assumptions are that each difference represents a mutation and that

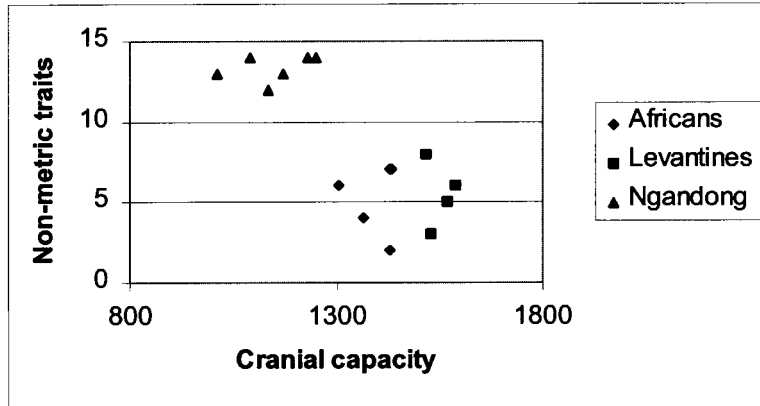


Figure 1. Robustness and cranial size. The relationship between presence of non-metric traits, presented here as the sum of their scores for each individual (following Lahr & Wright, 1996, Figure 10) and cranial size as measured by cranial capacity. The sum of the nonmetric scores is a measure of robustness because each was scored as a “0” or “1”, and whenever robustness characterized the difference, the more robust condition was scored as “1”. The geographic affinities of the groups being compared provide the main source of variation.

individuals who share fewer pairwise differences are more closely related because fewer mutations separate them. A similar assumption underlies all phenetic clustering techniques, where similarity is assumed to reflect relationship. Such procedures consider individuals who cluster more closely to be more closely related to each other.

We use pairwise analysis here for a similar purpose, to examine the relationship of WLH-50 to the individuals in our comparative samples, based on the 16 nonmetric traits described in Table 4. Our nonmetric traits were scored as presence or absence, so that the differences could be validly combined without weighing one more than another.³ We calculated pairwise differences in nonmetric traits between WLH-50 and all specimens in the comparative samples of Africans, Levantines and Indonesians. The chance of a Type 1 error is high with this test only if WLH-50 is more similar in size to the

Ngandong sample and if the traits that are correlated with cranial size do not reflect geographic differences. Both these conditions may be rejected, as discussed below. If WLH-50 is exclusively related to Africans and Levantines, then the probability of it looking more like the Ngandong sample than these other two samples should be effectively zero.

It may be claimed that because the analysis is a phenetic procedure, it is insufficient to test the relationships of this set of specimens because it does not take into account the polarity of the character states when judging the level of similarity between specimens. However, determinations of character polarity cannot be made using geographic groupings, but must instead be made using assumed phylogenetic groups. The identification of an appropriate outgroup for polarity assignments is not a problem, but the definition of traits within the phylogenetic groups assumed by the replacement hypothesis introduces an unacceptable amount of homoplasy for cladistic analysis. In particular, since replacement assumes that Africans and Levantines are part of a single species, and Ngandong a separate

³A trait, say, scored with four character states could contribute as much to a pairwise difference analysis as three traits scored as present or absent. We realize that our non-metric characters are not formally equal to each other in complexity or heritability, but contend that our approach to scoring makes them as comparable as possible.

species, then only traits uniquely present either in Ngandong or in the group of Africans together with Levantines could be considered as synapomorphies, if they were present in WLH-50. However, there are only eight such traits in our nonmetric data. Of these eight character states that are uniquely in one sample, five are polymorphic within their samples, and only three are shared with WLH-50 (all three are shared between WLH-50 and Ngandong). Such a degree of homoplasy may itself suggest the conspecificity of the specimens involved, but we question the validity of this whole approach.

Another cladistic alternative is to consider each specimen as an individual operational taxonomic unit (OTU). However, besides compounding the problem of homoplasy, this would require that we treat individuals as nonreticulating evolutionary units. But we *know* that *some* of these specimens belong to the same species, and that many of the traits are both polymorphic within samples and polygenic in inheritance. In these circumstances, it is more than likely for individuals to inherit the genes for a trait, even if the trait itself is absent in one or both parents. Therefore the traits do not conform to the cladistic assumption that descent with modification is the process generating their variation.

For these reasons, a phenetic procedure is preferred. The pairwise difference analysis would refute a replacement hypothesis if WLH-50 is found to be more similar to Ngandong fossils than to Africans or Levantines. It remains unexplained how such a pattern of similarities could evolve by chance.

Results

Discriminant function analysis

The discriminant function analysis resulted in two functions that together assigned all known specimens correctly into their orig-

inally assigned group. These functions, as determined by stepwise analysis, are based on five of the original 21 variables [Table 3(a-b)]. The first discriminant function accounts for 99.1% of the among-group variance, and is highly significant ($P < 0.001$, Wilks' Lambda test). The second discriminant function accounts for the remaining 0.9% of the among-group variance, but is insignificant ($P = 0.192$, Wilks' Lambda test). These variables sort WLH-50 with the Ngandong group to the exclusion of either the African or Levantine group (Figure 2). For the first discriminant function, the squared Mahalanobis distance from WLH-50 to the Ngandong centroid is 18.15, while the distance to the next closest group centroid, Africans, is 74.48.

Including the second discriminant function, though it is insignificant, tends to pull WLH-50 away from all of the groups somewhat. The high score on this discriminant function for WLH-50 appears to reflect principally the long glabella-bregma distance for this specimen, which, though it exceeds every other specimen in the analysis, is most similar to the value for the largest African specimens. For both functions taken together, the squared Mahalanobis distance from WLH-50 to the Ngandong centroid is 42.5, while that to the centroid of the next closest group, Africans, is 91.7. Based on these data, classification of WLH-50 is significant at the 0.001 level.

Pairwise difference analysis

Figure 3 shows significant differences among the groups for pairwise differences from WLH-50. Six of the seven Ngandong crania are closer to WLH-50 than any other specimens, and the seventh is only separated from the others by one specimen (Skhul 9). WLH-50 is unequivocally closer to the specimens from Ngandong than to any other group in its nonmetric traits. On the average it possesses fewer differences from the

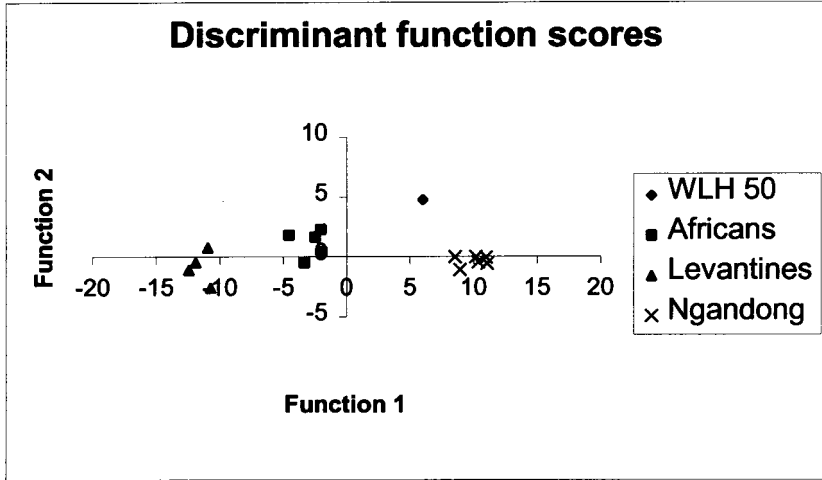


Figure 2. Discriminant function scores. The horizontal axis accounts for 99.1% of the among-group variance. Classification of WLH-50 is significant at the 0.05 level.

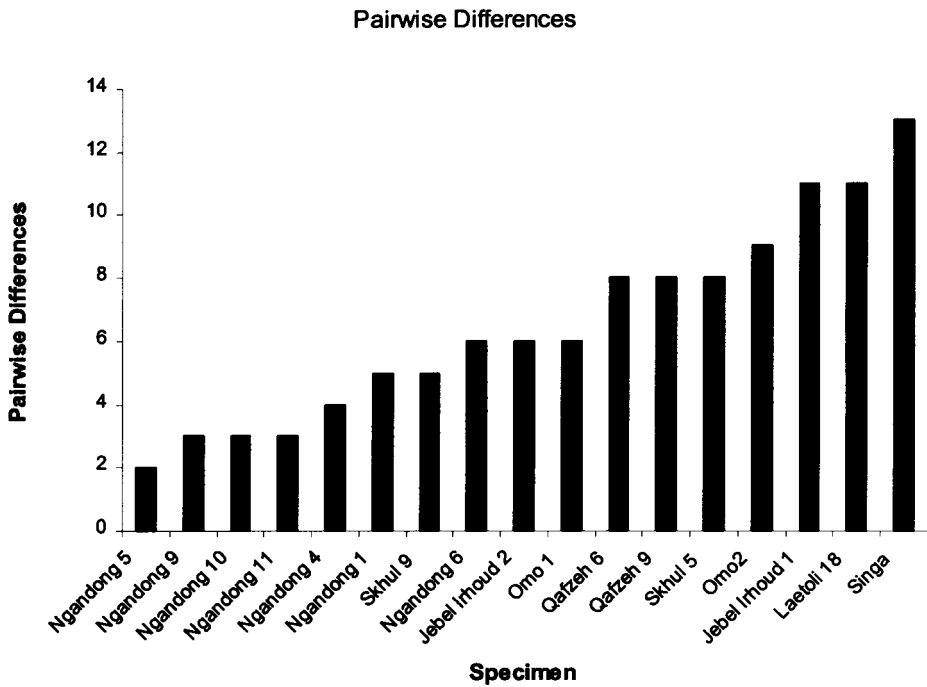


Figure 3. Pairwise comparison of WLH-50 to Indonesian, African and Levantine specimens. Mean pairwise differences between Ngandong and African, and Ngandong and Levantine groups are statistically significant at the 0.05 level (Wilcoxon–Mann–Whitney Test). The distribution of differences for Ngandong differs from the others ($P \leq 0.01$, sign test).



Figure 4. Ngandong 1 (left) compared with WLH-50 (center, cast) and Qafzeh 9 (right, cast), shown in lateral view to the same scale. The fundamental question this paper addresses is which two are alike and which one is different? According to [Stringer's analysis \(1998\)](#) the most similar pair is WLH-50 and Qafzeh 9. His illustration of WLH-50, said to support this, is not part of a comparison with other specimens, and is presented tilted more forward than our best estimate of Frankfurt Horizontal, accentuating the forehead height. We believe our comparison and the comparison in [Figure 5](#) provide a different answer.

Ngandong group (3.7 pairwise differences) than from either the African (9.3) or Levantine (7.25) groups. The Ngandong mean pairwise difference from WLH-50 is significantly lower than both the African mean and the Levantine mean differences (Wilcoxon–Mann–Whitney test). WLH-50 is most different from the Africans. However, the difference between the African and Levantine samples in the number of pairwise differences from WLH-50 is not significant.

Discussion

The results of both our analyses seem to unambiguously refute the replacement theory. There is no evidence suggesting WLH-50 can be grouped with either Late Pleistocene Africans or Levantines, to the exclusion of the Ngandong sample. To the contrary, WLH-50 is metrically and morphologically more like the Ngandong sample than it is like hominids from the other two regions. We might expect these findings if WLH-50 is a descendant of all three groups, whether or not the influence of Ngandong was stronger than the other two as the data

suggest. The results involve two different analyses of many different variables, and are not possible if the Levant and African samples are uniquely ancestral to WLH-50 while Ngandong, or some other sample like it, is not.

The concordance of both metric and non-metric analyses is important, because these two sources of evidence address morphological relationships in different ways. The metric analysis considers both the size and the shape of the crania under consideration, while the nonmetric analysis considers some factors that are independent of size or shape and allows comparisons of individual specimens. For the nonmetrics that do show some relationship to cranial size, this relationship depends on the populations being compared, and may be positively related, negatively related, or unrelated between samples of recent populations. This linkage to geography makes them appropriate tests of geographic affinities.

Yet [Brown \(1998\)](#) and [Stringer \(1998\)](#) reach different conclusions about the position of WLH-50, and it is worthwhile examining why these authors have accepted what visual inspection so readily rejects ([Figures 4 and 5](#)).

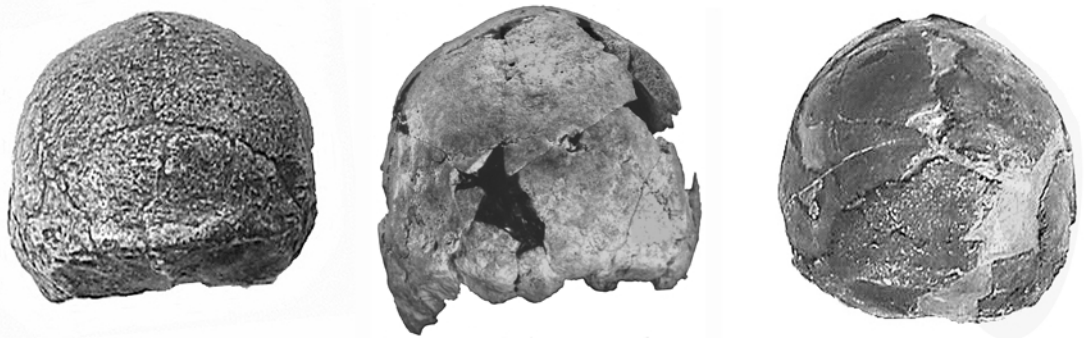


Figure 5. Posterior view of Ngandong 5 (left), WLH-50 (center), and Qafzeh 9. The central figure, WLH-50, is reproduced from [Brown \(1998\)](#), with his permission, and the other two are casts. All three are oriented in the Frankfurt Horizontal and are shown to the same scale. Once again the question is which two are the same, and which stands out as being different? We do not believe that WLH-50 and Qafzeh 9 are the most similar, as the replacement hypothesis would claim.

Different anatomy reported

Brown's anatomical observations do not always conform to our own, and we believe the differences are significant. In particular Brown makes two key points that are incorrect.

He asserts

“there is certainly no backward extension of the supraorbital region at the outer corner of the orbit, along with the temporal line, forming a knob-like trigone.”

This feature, named the frontal trigone by [Weidenreich \(1951\)](#), is common in and virtually unique to the Ngandong sample ([Figure 6](#)), and its absence in WLH-50 would be significant.

But while the outer corners of the lateral torus with the temporal lines are missing on both sides (the WLH-50 supraorbital breadth in [Table 5](#) is Brown's estimate), the angled edge between the anterior and superior surfaces of the lateral torus can be seen. On the left side, where the lateral torus is better preserved, as this edge is traced laterally to the break it progresses in a posterior and superior direction. The surface of the lateral torus forms part of a triangular prominence in this position, with the medial edge of the structure as described above

and with its apex oriented in the supero-posterior direction. The tip of the temporal line can just be seen: it is preserved on the bit of lateral edge remaining. In specimens lacking a frontal trigone, this edge passes laterally and inferiorly as it rounds the outer corner of the torus, and there is no prominence in this position. The WLH-50 anatomy is not complete, but the existing portion is clearly the medial edge of a small frontal trigone.

Second, Brown claims that

“although the inion region was undoubtedly large, what is preserved does not resemble the pronounced inferiorly pointing triangle present at Ngandong.”

Again, we differ with this assessment. The posterior of the vault is badly eroded and no cortical bone remains. Yet it is possible to see the outline of a nuchal torus that extends across the entire occipital bone, with its inferior edge defined by the prominent superior nuchal line and in many places its superior edge defined by the supreme nuchal line ([Figure 5](#)). Even though the supreme line cannot always be seen because of the erosion, the supratotal sulcus crosses the entire occipital bone, from one angular torus (on the temporal, paralleling the



Figure 6. Right lateral supraorbital region of Ngandong 9 showing the frontal trigone (after Weidenreich, 1951).

lambdoidal suture) to the other. We do not know how far posteriorly the nuchal torus extended because the bone surface is gone, but the presence of a supratoral sulcus and the existing anatomy suggest there was significant rearward projection. The inferior border of the torus outlines a prominent, downward-facing tuberculum linearum that follows the contour of the bone, and an occipital crest can be seen inferior to it, for a short distance until the broken base is encountered. Taking the erosion and missing bone surface into account, it would be fair to say there is no other region in the anatomy of WLH-50 that more closely resembles the Ngandong condition.

Apart from these points, Brown does not think WLH-50 is representative of late Pleistocene Australians and presumably believes its anatomy does not address their ancestry in any event. We discuss this further below.

Different methodologies: addressing the relation of size and robustness

Stringer (1998) demonstrated that WLH-50 is a modern human cranium, and we accepted this as we had concluded the same. However, for the replacement hypothesis to be correct, modern humans as a group including WLH-50, Africans, and Levantines must exclude Ngandong.

Stringer's analysis asserts this. It makes WLH-50 out to be more like the Qafzeh sample than any other group, including living Native Australians, and least like Ngandong. Here we cannot concur (Figures 4 and 5). It may be that differences between this study and our own stem from a discrepancy in data. Stringer's maximum frontal breadth measurement for WLH-50 (117 mm) is incorrect and probably is the *minimum* frontal breadth of the specimen. Instead, our maximum frontal breadth measurement (124 mm), taken on the coronal suture, is a conservative value for this variable.

However, a more significant difference between our study and Stringer's is the method of analysis. Much of this difference comes from his attempts to eliminate size and its influences. The issue is whether robustness is a function of size, as Lahr & Wright (1996), Brown (1989) and others have suggested. This question surely has different answers at different levels of analysis. For instance, *within* populations there is usually a clear relation between size and robustness because males are on average and in particular larger and more robust than females. It is quite possible that this is the fundamental relationship that Lahr & Wright (1996) show in their analysis. *Between* populations, on the other hand, the relationship could be just the opposite; this depends on which populations are compared. We examined the influence of size on the robustness between our comparative samples. We chose endocranial capacity to estimate cranial size because it is not based on any particular measurement used in our analysis. This helps to avoid spurious correlations that result from using different measurements of the same thing as independent and dependent variables (Solow, 1966), such as cranial length and brow ridge projection, or cranial breadth and parietal thickness. Ngandong is the smallest of our groups, but the most robust (Figure 1). A

similar relation can be found in other population comparisons; the population with larger crania is not always the more robust one.

Nevertheless, like many other investigators [Stringer \(1998\)](#) attempts to eliminate size from his analyses and consider only the shape-related components of metric variables (presumably, what is left after size is “eliminated”). There are two problems with such an approach. First, it is fairly clear that standard procedures for removing the effects of size correlation do not accomplish their goal. A principal component analysis, which Stringer uses, rotates the intercorrelation matrix for the data. It typically produces one general factor and a series of bipolar factors in which each variable tends to have a high coefficient (loading) for one axis, while each factor has low or zero coefficients for some of the variables. The analysis is therefore used to reveal structure in the intercorrelation matrix. The first principal component of a craniometric analysis, the general factor, is traditionally assumed to represent overall size in craniometric analyses. In Stringer’s analysis the first component reveals the archaic samples to be closest to WLH-50 (Ngandong and his “archaic Africans”), but this result is discarded because it is believed to be due to size.

Indeed the first component may account for many of the correlations of variables with overall cranial size. However size is multi-dimensional in its effects of craniometric data, effects that may be linear on some variables, nonlinear on others, and are usually interactive. [Pearson and colleagues \(1998:655–656\)](#) note:

“if a researcher wishes to investigate between-group differences, failing to consider the first principal component may be inadvisable. In fact, the first component usually captures size as well as between-group differences that mark some of the largest or smallest-sized OTUs (i.e., shape that is correlated with size).”

Some of the craniometric variables contribute to size more than others, and many intercorrelations accounted for in the first principal component may have nothing to do with size. Thus it is far from clear what size means when it is defined as the general factor. Again citing the [Pearson et al. \(1998:656\)](#) discussion of the first principal component, its

“aspects of between-group differences are thus correlated with size, but they may not necessarily result from allometry. Arguably, such differences should not be discarded after being summarily ascribed to size.”

Furthermore, standardizing variables for size with specimen means as Stringer does (the division of all elements in each row by the mean for the row), and then performing a principal components analysis, accounts for size only if different variables are isometrically related, which is not likely for craniometric data. It is not that these producers do not produce results (components, coefficients, and patterns) because they do, as they must. The question is whether these results can possibly be interpreted in any biologically (evolutionary) meaningful framework.

Second, there is no *a priori* reason to think that size is unimportant in all tests involving how fossils are related. To the contrary, there is some reason to believe that size plays a role in the relationships we are testing ([Figure 1](#)), because if we use endocranial volume, the Ngandong sample is the smallest of the three comparative groups while, as many have pointed out (see below), WLH-50 is a large cranium in many respects. This makes a test that rejects the replacement hypothesis if the closest relation of WLH-50 is with Ngandong a *conservative* test. It follows that both the size and shape of WLH-50 are of interest. The size question must be considered in reference to the hypothesis being tested, it may be important to eliminate size for some, but invalid for others.

Table 5 Comparison of WLH-50 with other large Late Pleistocene and Holocene Australian crania

	WLH-50	Coobool 50·5	Coobool 50·76	Cossack
Cranial length	212	207	211	221
Biparietal breadth	142	144	145	145
Supraorbital breadth	131	122	129	

All measurements are in millimeters.

Use of the discriminant function analysis to address the combined questions of difference between the samples and similarity of WLH-50 does not require us to interpret correlations between variables in terms of size or shape. Instead, the analysis produces a discriminant function that maximizes group cohesion, including the variables that can best sort specimens according to group membership. We have shown that the resulting variables are those that are associated with geography in the comparative sample. This is why the discriminant function approach is comparable with a visual inspection while the various manipulations of principal components analysis are not.

The non-metric analysis has the advantage of allowing us to examine some characteristics of the crania that are independent of their size. It might be claimed that certain nonmetric features reflect a pattern of greater muscle attachments on more robust crania, and that this robusticity is related to size. However, our data show no evidence that this suggestion is true in general. Our data show that some of the largest crania are the least robust. Using cranial capacity as a proxy for cranial size, none of the nonmetric features that we examined show significant associations with size within geographic regions. Instead, the features seem to be associated with the geographic regions themselves. As such, they outline regional patterns of robusticity, and may be useful indicators of the geographic affinities of the groups.

Representation issues

Setting these questions of data error and appropriate analyses aside, there are two different reasons why various authors have suggested WLH-50 may not reflect normal variation in Late Pleistocene Australians. If WLH-50 can be distinguished from Pleistocene Australian natives for reasons of anatomy or pathology, it may not be a valid test of the replacement theory for living indigenous Australians.

The first issue is about whether the vault is unusually large and thereby unrepresentative. [Brown \(1998\)](#) asserts that

“the extremely large size of WLH-50 should be of some concern to those who argue that this skeleton is in some manner representative of ‘Late Pleistocene’ Australians.”

He suggests that an unusual size for WLH-50 could create the elements of robustness whose manifestations cause it to appear similar to Ngandong. As we discussed above, if there was such a size difference, its consequences may well be expected to differ from this assertion, but in any event, some of the Australian crania dated to the terminal Late Pleistocene or Holocene from Coobool Crossing (that [Brown himself studied, 1989](#)), as well as others such as Cossack ([Freedman & Lofgren, 1979](#)), are as large as WLH-50, or for some dimensions even larger (Table 5, using published measurements).

In fact, there are many anatomical similarities linking WLH-50 not only with Ngandong, but with later Pleistocene



Figure 7. Posterior view of Coobool Crossing 50.76. This large cranium (Table 5) has a posterior contour very similar to WLH-50, with the greatest breadth across the supramastoid region at the cranial base. If the gamma spectrometric data is correct (Simpson & Grün, 1998), these two specimens may be penecontemporary, but in any event the anatomy of WLH-50 is not unique among Late Pleistocene/Holocene native Australians.

Australians as well. Coobool Creek 50.76, like WLH-50 and the Ngandong specimens (and many other Pleistocene hominids), has its greatest cranial breadth across the cranial base, and the greatest parietal breadth low on the bone, near asterion (Figure 7). Some Late Pleistocene and Holocene Australians like this specimen and others (Coobool Creek 50.35, Kow Swamp 1, etc.) have a true, unbroken supraorbital torus (Figure 8). These observations show that some kind of link with Ngandong would be a credible interpretation of Lake Pleistocene Australian variation, even if WLH-50 had never been found. They also show that the anatomy of WLH-50 is not unexpected in a Late Pleistocene Australian cranium.

These relationships were recognized a decade before WLH-50 was discovered, when a nonmetric study of recent crania by Larnach & Macintosh (1974) compared a number of Australian and New Guinea crania with Europeans and Africans, scoring them for the 18 characters that Weidenreich (1951) claimed were unique in the Ngandong hominids. Six of these were absent in all modern samples, but nine of the 12 other features were found to attain their highest frequencies in the Australian and New Guinea natives. These frequencies are fairly low, but there are similar findings of a greatly reduced percentage of very common Neandertal features found in living Europeans (Frayer, 1993), and combined, these observations from different geographic

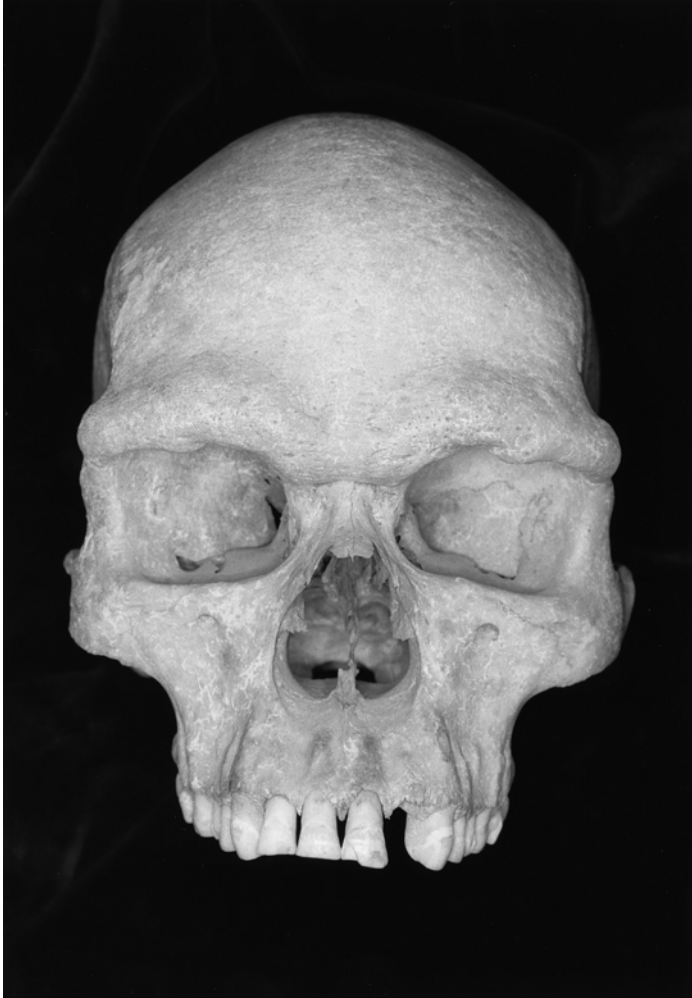


Figure 8. An unbroken, true, supraorbital torus and wide interorbital area are not uncommon in Late Pleistocene and Holocene Australians and may be found in recent Native Australians such as cranium 3596 from Euston, shown here. This geographic distribution demonstrates that the features are regional and cannot be used as markers of “evolutionary status” because by observation and definition no living human group can be more “advanced” than another.

areas may provide an accurate reflection of the magnitude of Holocene skeletal change.

The second issue is about the possibility of pathology, and its potential influence on the size and shape of the cranium. There have been attempts to explain the unusually thick vault of WLH-50 as an adaptive response to some sort of chronic anemia or a related pathology (Brown, 1989, 1992; Webb, 1990; Pardoe, 1993), and this has

been used to invalidate comparisons with the cranium because its form could be altered, albeit in unknown and unspecified ways. Webb suggests that the intracranial bone structure of WLH-50, which is marked by the presence of thin inner and outer cortical tables contrasted by thick diploic or cancellous tissue in between, is an adaptation brought on by the need for hematopoietic reinforcement. The proposed anemic

condition which created this need is perhaps closely related to, or a precursor to, modern genetically derived hemoglobinopathies, such as sickle cell anemia or thalassemia. The conditional tone of Webb's assertion is due to the fact that WLH-50 does not display skeletal changes conforming to those observed in recent populations suffering from genetically determined anemias (Webb, 1990; Armelagos, personal communication). WLH-50 lacks any overt expression of symmetrical hyperostosis, cribra orbitalia, or localized bossing of the parietal or frontal squamae, which are the main paleopathological indicators of chronic anemia.

Webb states that the Late Pleistocene Singa calvarium from the Sudan is the only other known example, either archaic or modern, of such unusual cranial thickening. But in their analysis of the Singa cranium *Stringer et al.* (1985) conclude with a prognosis similar to ours:

“with the exception of the diplöic thickening, the Singa skull did not exhibit any of the other radiographic criteria associated with bone changes in anemia. There was also no sign of porotic hyperostosis. On the basis of these results there is little to support the hypothesis that anemia was responsible for the unusual shape and diplöic thickening seen in the Singa skull.”

Stringer (1998) went on to use Singa's cranial measurements as part of his archaic African sample, and we follow him in including this specimen in our sample. Furthermore, if WLH-50 and Singa are found to share a similar pathological condition that results in thickened cancellous bone, this condition could not account for the anatomical similarities of WLH-50 and Ngandong because the anatomy of Singa is the most different from WLH-50 of any comparable specimen (Figure 3).

If diplöic thickening of WLH-50 were the result of chronic anemia, the hemoglobinopathy responsible would have to be unlike

any known today or throughout paleoepidemiological history. For this reason, a pathological explanation of the vault thickening in WLH-50 is tentative at best. Other explanations for the morphology include a combination of advanced age (cranial thickness increases with age) and normal population variation, in this case similarity to the wide ranges of variation in Australian fossil hominid samples such as Coobool Creek (*Miller, 1991*). *Webb* (1989) notes that variation in several features among the Willandra hominids exceeds that of other fossil samples such as Ngandong and Zhoukoudian. But in each of these samples the form of the variation is limited to a distinct pattern; for instance, the frontal trigone at Ngandong, or the large percentage of diplöic bone in relation to total cranial thickness at Willandra, 73% for WLH-50, which is the same as Mungo 3 and less than several other Willandra specimens (data from *Webb, 1989, Table 3*).

Plesiomorphy

A final issue concerning the analysis is the possibility that one might view the similarities between WLH-50 and Ngandong as plesiomorphic. Though we use a noncladistic approach, it remains possible that any of the similarities between WLH-50 and the Ngandong sample might be thought of as primitive retentions from a distant common ancestor. If this were true, then our tests might reject a unique ancestor–descendent relationship between WLH-50 and Late Pleistocene Africans and Levantines purely on the basis of a more distant relationship with Late Pleistocene Indonesian hominids.

Since we considered Late Pleistocene samples that are potentially ancestral to WLH-50, by virtue of the hypotheses we examine and their age relative to this specimen, we can view the issue of plesiomorphy without recourse to a more distant outgroup. Simply put, for a feature that tends to link WLH-50 with the Ngandong to be a

plesiomorphic retention, it must be present in the putative African and Levantine ancestors of WLH-50. But while some features linking WLH-50 to Ngandong are polymorphic in the Africans and Levantines, others are not. There are three nonmetric features in our data that are present in WLH-50 and the Ngandong sample and absent in the other samples. These are a transversely extensive nuchal torus, a projectinginion, and a lateral frontal trigone. For these traits to be plesiomorphic, they must have existed at an as-yet-undetected frequency in the African or Levantine ancestors of WLH-50. In contrast, there is no character state that is present in WLH-50 and Africans or Levantines and absent from the Ngandong sample. It might therefore be easier to make an argument of plesiomorphy in the other direction, though this is not our aim.

Alternatively, it is possible that the features uniquely shared by Ngandong and WLH-50, other features that are rare in the African and Levantine samples but frequent in Ngandong and present in WLH-50, and detailed set of metric similarities between Ngandong and WLH-50, reflect parallel evolution. Though we find it difficult to imagine a scenario in which this set of similarities between early and late specimens in Indonesia and Australia could evolve by chance, other workers may find justification for this alternative. However, since the criterion guiding phylogenetic systematics is parsimony, it would seem necessary to consider the least refuted hypothesis as the most parsimonious alternative. In this case, the most parsimonious explanation for the similarities among these groups is surely the conspecificity of all the specimens involved. A reticulating evolutionary relationship can explain both the presence of shared traits between WLH-50 and Ngandong and the fact that WLH-50 and Late Pleistocene Africans and Levantines are modern humans. Since there is no reason to reject such a hypothesis and no reason to accept an

alternative to it, as our analysis shows, we should consider all these specimens to be members of a single reticulating species. The implications of this hypothesis are discussed in the following section.

Significance for Ngandong

If total replacement is the wrong explanation for the morphology of recent humans in this region of the world, what are the implications for Ngandong? Our analysis shows there are significant similarities between WLH-50 and Ngandong, but there are ample differences as well and we do not claim, or believe, that WLH-50 could be considered part of the Ngandong sample (Thorne *et al.*, in preparation; Webb, 1989). Moreover, these similarities do *not* imply that Ngandong is the sole ancestor of Native Australians. An explanation like that is similar to Haeckel's or Coon's polygenism and requires unjustified belief in the power of parallel evolution⁴ (Wolpoff & Caspari, 1997). On the other hand, the multiregional interpretation that Ngandong is *among* the ancestors of Native Australians fits well with the several hypotheses of multiple origins for Native Australians developed over the years (Birdsell, 1967; Macintosh, 1963; Thorne, 1977). It is compatible with the contention that Ngandong is an intermediate between the earlier Kabuh Indonesians and Native Australians in the sense that, as Weidenreich (1943) put it,

“at least one line leads from *Pithecanthropus* and *Homo soloensis* to the Australian aborigines of today. This does not mean . . . all the Australians of today can be traced back to *Pithecanthropus* or that they are the sole descendants of the *Pithecanthropus*–*Homo soloensis* line” (pp. 249–250).

⁴Polygenism seems to be the hypothesis a number of authors try to disprove when they address multiregional evolution (cf. Tishkoff *et al.*, 1996; Chu *et al.*, 1998; Cavalli-Sforza, 1998). Multiregionalism is persistently, and incorrectly, described as multiple origins (see Wolpoff & Caspari, 1997).

However, in the recent redating of Ngandong (Swisher *et al.*, 1996), it was claimed that Ngandong cannot be such an intermediate because

“*Homo erectus* from Ngandong overlaps in time with *Homo sapiens* from Australia.”

There is a problem here, because even if there was such an overlap, Ngandong could reflect a transitional anatomy for two different reasons: (1) as a direct ancestor of some Pleistocene Australians,⁵ or (2) as a mutual descendent of a common ancestor with Native Australians. *Both* could be correct, but if *either* is correct Ngandong cannot be “*Homo erectus*”, according to a definition of species that relies on branching. Radiometric dates cannot invalidate the anatomical interpretation that Ngandong is (or is related to) an Australian ancestor, unless one is willing to accept the premise of polygenism and assume that the Australians were a unique human line that became isolated from the rest of the world once Australia was colonized. Otherwise, Indonesia could have continued to contribute colonists descended from Ngandong.

The possibility that Ngandong can be in the middle of the Late Pleistocene, and be “*Homo erectus*” and be among the ancestors of Native Australians is rendered implausible by the dates. To be valid, this would have to mean that “*Homo erectus*” in this region became *H. sapiens* later than in other parts of the world—a contradictory and biologically invalid interpretation that is unacceptable. To circumvent it, there are those who admit to the resemblances, but argue that they lack taxonomic significance because they are “plesiomorphic” since Ngandong, which the Australians resemble, is “*Homo erectus*”. If so, the argument continues, the resemblances cannot describe regional continuity because relationships

⁵This could be in the sense of a last common ancestor, or in the sense of an older common ancestor, some of whose Javan descendants were Australian colonizers.

Table 6 Brain volumes in cubic centimetres

	Female average	Male average
Indonesian Kabu	875 (<i>n</i> =5)	1032 (<i>n</i> =2)
Indonesian Ngandong	1093 (<i>n</i> =2)	1177 (<i>n</i> =4)
Native Australian	1119 (<i>n</i> =22)	1239 (<i>n</i> =51)

should not be based on plesiomorphic features.

But this whole line of argument is fallacious because it follows from the assumption that the human groups compared evolved independently. Without making this assumption, as we noted above the phylogenetic descriptions like apomorphy and plesiomorphy can not validly apply. Moreover, how can common anatomy in recent Native Australians be more plesiomorphic than different anatomy in other recent human populations, as would have to follow from this argument, without interpreting the difference to mean that some human populations differ from others because they have more genes from an extinct primitive human species? The weight of the data suggests that the problem, and its solution, lie in the taxonomy.

Ngandong differs from its Kabuh ancestors and approaches the anatomy of Late Pleistocene *H. sapiens* elsewhere in many ways. For instance, it has significant supraorbital torus reduction (comparing like sexes, the torus is smaller than the Kabuh specimens, and a depression over the nose results in its distinct separation into right and left sides). The frontal bone is markedly broader, especially across the frontal lobes (behind the orbits, where the postorbital constriction is less). The articular eminence for the mandible is projecting and well defined. The occipital plane of the occipital bone is markedly expanded while the nuchal muscle attachment area is decreased by some 30%. But most importantly the relationship can be seen in brain size (Table 6).

The Ngandong sample has a brain size considerably expanded over the Kabuh hominids, not just within the Native Aboriginal Australian *range* but closely approaching the *mean*.

These common changes would have to be explained by parallelism if “*Homo erectus*” persisted on Java while *H. sapiens* was evolving the same way in other places. One complex parallelism is possible but combined these pose a statistical improbability.

We do not believe any of this is correct. WLH-50 and other Australian Late Pleistocene fossils are modern humans, and the clear implication of their links to Ngandong is that these older Indonesians are *H. sapiens* as well.

Conclusion

The WLH-50 calvarium is vitally important to the understanding of modern human origins in Australasia (Thorne *et al.*, in preparation; Webb, 1989). We used it in a test of the complete replacement model in the region, which predicts that Late Pleistocene Africans and Levantines are direct ancestors of WLH-50, while the Ngandong hominids cannot be. Two distinct procedures, a discriminant analysis of metric data for the groups and a pairwise difference analysis of nonmetric data for individuals, were used to test this model. Both tests clearly refuted complete replacement in Australasia. In addition, both methods yielded statistically significant results, which seemingly indicate that similarities between the Ngandong fossils and WLH-50, a modern human, are phylogenetic.

Given their geographic and temporal distribution, the Ngandong hominids were most probably one of the ancestors of WLH-50, as would be predicted under a multi-regional model of human evolution. These findings call into question prior classification of the Ngandong hominids as a separate evolutionary species, *H. erectus*, and indicate

that they should be included within the species *H. sapiens*.

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