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ABSTRACT

The debate surrounding the initial appearance of anatomically modern *Homo sapiens* and subsequent evolution into modern *Homo sapiens sapiens* had centered on two competing hypotheses. The "Multiregional Continuity Model" and the "Out of Africa 2 Model". Evidence for these models has primarily come from analyses of pertinent fossilized remains and genetic data. White et al. (2003) suggests that their multivariate analyses of one of three fossil crania, from the Herto formation of the Bouri member in the Middle Awash, Ethiopia, places the fossil intermediate between archaic *Homo sapiens* (i.e., Kabwe) and more modern *Homo sapiens* (i.e., Qafzeh and Skhul V). This, White et al. (2003) suggests, would be strong evidence for the "Out of Africa 2 Model", albeit in a somewhat gradualistic sense. The purpose of the study undertaken here is to reanalyze the Herto specimen (i.e. BOU-VP-16-1) using c-score (i.e., shape) principal coordinates and Euclidean distances to determine if the Herto cranium is morphometrically intermediate between archaic *Homo sapiens* and more modern *Homo sapiens sapiens*. Our results indicate that indeed these data can be reduced to show that the Herto cranium is relatively similar to our Upper Paleolithic *Homo sapiens* sample, Skhul V, and our modern *Homo sapiens sapiens* sample, in that order. Furthermore, our analyses suggest that Herto is not intermediate between Kabwe and more modern *Homo sapiens*.

INTRODUCTION

The debate regarding the origins of anatomically modern *Homo sapiens* had primarily focused on two competing hypotheses, the "Multiregional Continuity Model" and the "Out of Africa 2 Model" (Stringer 2002; Trinkaus 2005; Wolpoff et al. 2001). These two models had dominated the discussion regarding the origin(s), evolution and migration of anatomically modern *Homo sapiens*. However, in recent years these models have been supplanted by a more recent amalgamation of the two models, the "Assimilation Model" (Smith et al. 1989).

The "Multiregional Continuity Model" proposes that anatomically modern *Homo sapiens* evolved *in situ* in Africa, from *Homo rhodesiensis* (i.e., African archaic *Homo sapiens*); in Europe, from Neanderthals (i.e., European archaic *Homo sapiens*); and in Asia, from *Homo erectus* (Frayer et al. 1993; Wolpoff et al. 1994; Xinzhi 2001). Support for this model is based on the continuation of skeletal traits from "archaic" specimens into the respective modern populations (Frayer et al. 1993; Wolpoff et al. 1994; Xinzhi 2001). For example, in Europe it is suggested that the retention of the retro-molar space in the mandible, from Neanderthals to modern *Homo sapiens*, was an indication of shared ancestry (Frayer et al. 1993). Furthermore, this model hypothesizes that, during the sapienization process (i.e., the progression towards *Homo sapiens sapiens*), there was restricted gene flow between the separate geographic populations (i.e., Africa, Asia, and Europe). Therefore, the limited transfer of genetic material between geographic centers of sapienization prevented these subgroups from diverging into separate species (Etler 1996; Frayer et al. 1993).

Opposing this model is the "Out of Africa 2" or 'Replacement Model". This model suggests that anatomically modern *Homo sapiens* evolved first in sub-Saharan Africa and then migrated into Asia and later into Europe (Rightmire 1988; Stringer 1993 & 1994). In this model archaic forms of the genus *Homo* were replaced by more modern forms. Relethford (1998) and Templeton (2002) suggest, based on the genetic data, that the origin of anatomically modern *Homo sapiens* was most likely in sub-Saharan Africa. Furthermore, Relethford (1998) suggests that the greater within-group genetic diversity (i.e., 85-90%) among modern sub-Saharan Africans implies they either had a larger long-term population size or they are genetically the most distant populations (i.e., the oldest populations). Stringer (2002), Templeton (2002), Trinkaus (2005), and White et al. (2003) all suggest that anatomically modern *Homo sapiens* first began to evolve from more "archaic" forms of *Homo sapiens* (i.e., *Homo rhodesiensis*) in East Africa before 130,000 years ago.

Nevertheless, Templeton (2002) and Trinkaus (2005) went on to suggest a probable scenario where anatomically modern *Homo sapiens* both interbred with and replaced "archaic" forms of *Homo* (i.e., Neanderthals and Asian *Homo erectus*) as they expanded out of Africa. This "Assimilation Model", which includes aspects of both continuity and replacement, has been gaining acceptance since Smith et al. (1989) first proposed it (Hawks and Wolpoff 2003; Relethford 1998; Smith 1994; Templeton 2002). The "Assimilation Model" suggests an African origin for anatomically modern *Homo sapiens* with both interbreeding, and replacement taking place as more "archaic" forms in Asia and Europe are replaced during the migration of *Homo sapiens* out of Africa (Smith et al. 1989). This model has gained further support with recent comparisons of Neanderthal DNA and modern *Homo sapiens sapiens* DNA, which indicates that Neanderthals did contributed to the gene pool of modern *Homo sapiens sapiens* primarily in Europe (Green et al. 2010).

With this growing consensus towards Africa being the birth place of anatomically modern *Homo sapiens* our focus must shift towards an understanding of the relationships

between Middle and Late Pleistocene African fossil crania and their implications for the transformation from archaic forms of *Homo sapiens* to more modern forms of *Homo sapiens*. Trinkaus (2005) suggests that the development of anatomically modern *Homo sapiens* took place from approximately 150,000 to 50,000 years ago in Africa. During this time modern *Homo sapiens* traits arose sporadically in a mosaic pattern throughout Africa and were transferred between populations as the results of gene-flow (Trinkaus 2005). This mosaic pattern of traits eventually evolved into a suite of traits that are characteristic of fully modern *Homo sapiens sapiens* by 40,000 years ago (Trinkaus 2005).

Among the earliest potential ancestors of anatomically modern *Homo sapiens* are Omo Kibish 1 (<195,000 B.P.), Herto (<160,000 B.P.), Singa (<150,000 B.P.), and Mumba (<130,000 B.P.) (Trinkaus 2005). However, the Herto specimen (BOU-VP-16/1) is unique among these crania, due to the fact that it is relatively complete, it is an adult, and it is not deformed due to pathology (Trinkaus 2005; White et al. 2003). Thus, the Herto adult cranium is the oldest and most complete early potential example of an evolutionary trajectory towards anatomically modern *Homo sapiens*, which makes it especially useful for comparative analyses. Unfortunately, the original multivariate analyses of White et al. (2003) were based on only a few variables that lacked the morphology of the face. Furthermore, the analysis of White et al. (2003) has a complicated graphical presentation of the results which makes evaluation of their results difficult. For these two reasons we have chosen to reanalyze the Herto BOU-VP-16/1 cranium utilizing univariate, principal coordinate, and Euclidean distance analyses of craniofacial measurements. These craniofacial data will then be compared to a smaller modern *Homo sapiens sapiens* sample, as well as numerous other Middle and Late Pleistocene fossil crania from the genus *Homo*. The combination of neurocranial variables and facial variables should increase the accuracy of the results by increasing the number of variables employed and the use of a smaller number of individuals (i.e., smaller *H.s.s.* sample size) will allow for a less complicated and easier to understand graphical presentation of the results. Furthermore, we will corroborate the results of the principal coordinate analyses by comparing the results of principal coordinates to a Euclidian distance matrix.

The purpose of this research is to utilize univariate, principal coordinate, and Euclidian distance analyses to compare the adult Herto cranium (BOU-VP-16/1) to numerous individuals from Middle and Late Pleistocene hominin fossil record and a world-wide sample of modern *Homo sapiens sapiens* crania. The aim of this work is two-fold. First, it is to determine how the morphology of the Herto adult specimen fits within the broader Middle and Late Pleistocene hominin fossil record. Second, it is to determine if the Herto cranium is intermediate between East African archaic *Homo sapiens* (i.e., Kabwe) and modern *Homo sapiens sapiens*, as suggested by White et al. (2003).

MATERIALS AND METHODS

Materials

The total sample utilized for the principal coordinate analyses is composed of the individual specimens Herto, Kabwe, Skhul V, Steinheim, as well as a world-wide modern *Homo sapiens sapiens* sample (n=22), an Upper Paleolithic *Homo sapiens* sample (Cro-Magnon 1, Predmosti 3 & 4), an Asian *Homo erectus* sample, (Zhoukoudien 11 & 12), and a Neanderthal sample (Amud, Saccopastore 1, Shanidar). These specimens were chosen because they are Middle to Late Pleistocene or Holocene in age and they had the necessary measurements for comparative analyses. The modern *Homo sapiens sapiens* sample is composed of adult males

and females with African (i.e., Sub-Saharan and African-American), Asian (i.e., Central and Southeast), Native Australian, European (i.e., Euro-American), Native American (i.e., Central U.S. and Arctic), and Pacific Islander (i.e., Hawaiian) ancestry. For the Euclidean distance and univariate analyses a subset of the original data set were utilized, including Kabwe, Herto, Skhul V, the Upper Paleolithic *Homo sapiens* sample, and the *Homo sapiens sapiens* samples. These samples were chosen because they allow for a closer comparison of the relationship between Herto, Kabwe, and more modern *Homo sapiens*.

These data for the Herto specimen came from White et al. (2003). These data for Kabwe, Skhul V, Steinheim, Cro-Magnon 1, Predmosti 3 & 4, Zhoukoudien 11 & 12, Amud, Saccopastore 1, Shanidar, and *Homo sapiens sapiens* sample were all collected by RSC. These data consist of 27 craniofacial measurements utilizing the appropriate standard measuring instruments specific to each type of measurement (i.e., sliding calipers, spreading calipers, and tape measure) (Table 1). Cranial capacities were estimated for some modern *Homo sapiens* at 1450 cubic centimeters. This cranial capacity was utilized because it is the average (Conroy 2005) or above the average (Molnar 2006) for known modern humans. Utilizing the average or above average cranial capacity is designed to increase separation for this variable between fossil and modern members of the genus *Homo*.

Methods

First, the scores for all 27 variables for Herto, Kabwe, Skhul V, Cro-Magnon 1, and Predmosti 3 and 4 were compared individually to the range for *Homo sapiens sapiens.* These univariate analyses were undertaken in order to see how the individual fossil specimens compare to the range of variation for *Homo sapiens sapiens*. Next, these raw data, for the total sample, were standardized, then transposed, and then standardized again to in order to obtain a variant of "c-scores" (i.e., dimensionless shape alone) in SYSTAT 12. This process removes size from these data by standardizing each variable by a z score thus eliminating the effects of size differences brought about by variation between the sexes (Corruccini 1987). From these data all 34 specimens were compared utilizing all 27 variables in SYSTAT 12 in order to produce principal coordinates based on variation in shape. The first three principal coordinates were graphed using Microsoft Excel for two-dimensional graphs (Figures 1 and 2) and SPSS 18.0 for the three-dimensional graph (Figure 3). These analyses were undertaken to determine the relationship between these Middle and Late Pleistocene samples and the Holocene samples. Finally, these principal coordinate data were then utilized to develop Euclidean Distance matrix (Table 4). The Euclidian distance analyses were undertaken to confirm the results of the principal coordinate analyses.

RESULTS

Univariate

Based on univariate analyses Herto is within the range of variation of fully modern *Homo sapiens sapiens* for 70% (i.e., 19 of 27) of the craniofacial traits, including maximum cranial breadth, maximum frontal breadth, bistephanic breadth, bizygomatic breadth, biauricular breadth, basion-prosthion length, nasion-prosthion length, nasal height, nasal breadth, orbital height, orbital breadth, bimaxillary breadth, interorbital breadth, simiotic chord (i.e., least nasal breadth), bregma-lambda chord (i.e., parietal chord), biparietal breadth, inion-opisthocranion arc, bi-mastoid tip breadth, and cranial capacity (Table 1). Conversely, Herto does lie outside the range of variation of fully modern *Homo sapiens sapiens* for glabella-occipital length, basion-

nasion length, basion-bregma height, external palate breadth, biorbital breadth, foramen magnum length, nasion-bregma chord (frontal chord), and frontotemporale breadth. Of the Upper Paleolithic *Homo sapiens*, Cro-Magnon 1 has 88% (23/26) of its variable measurements falling within the range of variation for *Homo sapiens sapiens*, Predmosti 3 has 73% (16/22) and Predmosti 4 has 80% (20/25). Skhul V has 77% (22/26) of its variable measurements that lie within *Homo sapiens sapiens* range of variation. Kabwe, on the other hand, has only 50% (13/26) of its variable measurements within the range of variation of our *Homo sapiens sapiens* sample. This simple examination suggests that Kabwe is the most dissimilar from our modern *Homo sapiens sapiens* sample. The most similar to our modern *Homo sapiens sapiens* sample is Cro-Magnon 1 followed closely by Predmosti 4, Skhul V, Predmosti 3 and then finally Herto (Table 1). These analyses indicate that Herto is nearly twice as similar to *Homo sapiens sapiens* as Kabwe. However, and in line with expectations, all of our Upper Paleolithic *Homo sapiens* and Skhul V are more similar to *Homo sapiens sapiens* than the earlier Herto and Kabwe crania

	Herto	Kabwe	Skhul V	Cro-Magnon	Predmosti 3	Predmosti 4	*H.s.s.* Range
Glabella-occipital length	219.5	210	192	206	202	192	170.5-208
Basion-nasion length	110	112	98	104		99	94-108
Basion-bregma height	147.5	129	129	134	136	136	121-141
Maximum cranial breadth	155	144.5	143	153	143.5	144	126.5-160
Maximum frontal breadth	120	118.5	114	125	128	129	104-125
Bistephanic breadth	96.3			121	121	126	79-117
Bizygomatic breadth	142	147	145	140.5	144		119.5-144.5
Biauricular breadth	138	142	140	127	141	134	113-141
Basion-prosthion length	111	115	115	108	120	104	84-111
Nasion-prosthion length	79	95.2	73	71	77.4	65	60.2-81.5
Nasal height	56	59	53	52	59.9	48.5	41.1-60
Orbit height, left	34	39	30	27.5	31	30	31-39.1
Orbit breadth, left	42	51	46	45.5	46.7	41	37.5-46
Nasal breadth	29	31.1	28	22.5	26.4	28	23.2-29.2
Palate breadth external	75.5	78	69.5	68	68	61	58-71
Bimaxillary breadth	100	110	110	104.2		90	85-111
Biorbital breadth	126	123	111	106	107.3	98.5	91-108
Interorbital breadth	31	34	24				21.2-33.7
Simotic chord	8	12.5	7.2	9.8	9.9	9.8	3.1-13
Foramen magnum length	45.0	41	41.5	39		41	22.8-41.2
Nasion-bregma chord	124	121	106	125.2	120	114	102.5-120.5
Bregma-lambda chord	129	111	107	118.9	118.8	120.5	101-138
Frontotemporale Breadth	112	97.5	99	104.5	103	98.5	76-107
Biparietal Breadth	145	137	136	147	143	141	126-159
Inion-Opisthocranion Arc	48	59	26.5	43		30	25-60
Bi-Mastoid Tip Breadth	109	121.5	105.5	106	120	95	91-109
Cranial Capacity*	1450	1325	1510	1590	1608	1518	1250-1450*

Table 1: Measurements for univariate comparisons for Herto, Kabwe, Skhul V, Cro-Magnon 1, and Predmosti 3 & 4, as well as the range data for *Homo sapiens sapiens.* Numbers underlined fall within the range of variation for the *Homo sapiens sapiens* sample. These analyses show that Cro-Magnon 1 (88% of variables fall within *H.s.s.* range of variation) is the most similar in these variables to *H.s.s.*, followed closely by Predmosti 4 (80%), Skhul V (77%), Predmosti 3 (73%), Herto (70%), and finally Kabwe (50%).
* Some modern *Homo sapiens sapiens* individuals had cranial capacities estimated at 1450cc.

Principal Coordinates

The principal coordinate analyses produced a total of nine coordinates which explain 84 percent of the total variation within this overall sample. This led to the conclusion that the relationship between these variables is quite complex. For the purpose of this study, only the first three of these nine principal coordinates could be examined in detail due to limits of multidimensional hyperspace being graphically displayed. These three principal coordinates explain 54 percent of the total variation (Table 2). The first four variables that most strongly influenced each of the first three principal coordinates for both the positive and negative loadings are shown in Table 2.

	Positive loading	**Negative loading**
Principal coordinate 1 22.127%	Bregma-lambda chord (parietal chord) Cranial capacity Nasion-bregma chord (frontal chord) Maximum frontal breadth	Nasion-prosthion length Orbit height Nasal height Nasal breadth
Principal coordinate 2 17.424%	Orbit height Cranial capacity Nasal height Nasion-bregma chord (frontal chord)	Biorbital breadth Biauricular breadth Orbit breadth Glabella-occipital length
Principal coordinate 3 14.383%	Bregma-lambda chord (parietal chord) Orbit breadth Glabella-occipital length Biorbital breadth	Maximum cranial breadth Maximum frontal breadth Biauricular breadth Cranial capacity

Table 2: Positive and negative loadings for principal coordinates 1 through 3, underlined variables primarily drove the principal coordinate loadings.

These principal coordinate analyses have shown that Herto is most similar in these three principal coordinates to the Upper Paleolithic *Homo sapiens* sample, Skhul V, and modern *Homo sapiens sapiens*, in that order (Figure 3). When the Herto fossil is plotted against the other specimens in principal coordinates one and two we can see that the Herto specimen lies just outside the range of variation for our *Homo sapiens sapiens* sample in principal coordinate two (Figure 1). Principal coordinate one is predominantly controlled by neurocranial measurements, positively, and the size and shape of the middle to upper face, negatively (Table 2). The negative loading for principal coordinate two is most strongly controlled by the biorbital breadth, and less so by biauricular breadth, orbit breadth, and glabella-occipital length (Table 2). Biorbital breadth is much wider in Herto than *Homo sapiens sapiens* (Table 2). Our Upper Paleolithic sample lies on the border of this sample in these two principal coordinates and between the Herto specimen and the *Homo sapiens sapiens* sample (Figure 1). In Figure 1, Herto does not lie intermediate between the "archaic" members of the genus *Homo* (i.e., Kabwe, Neanderthals, and *Homo erectus*) and more modern members of the genus *Homo* (i.e., Cro-Magnon 1, Predmosti 3 & 4 and our *Homo sapiens sapiens* sample).

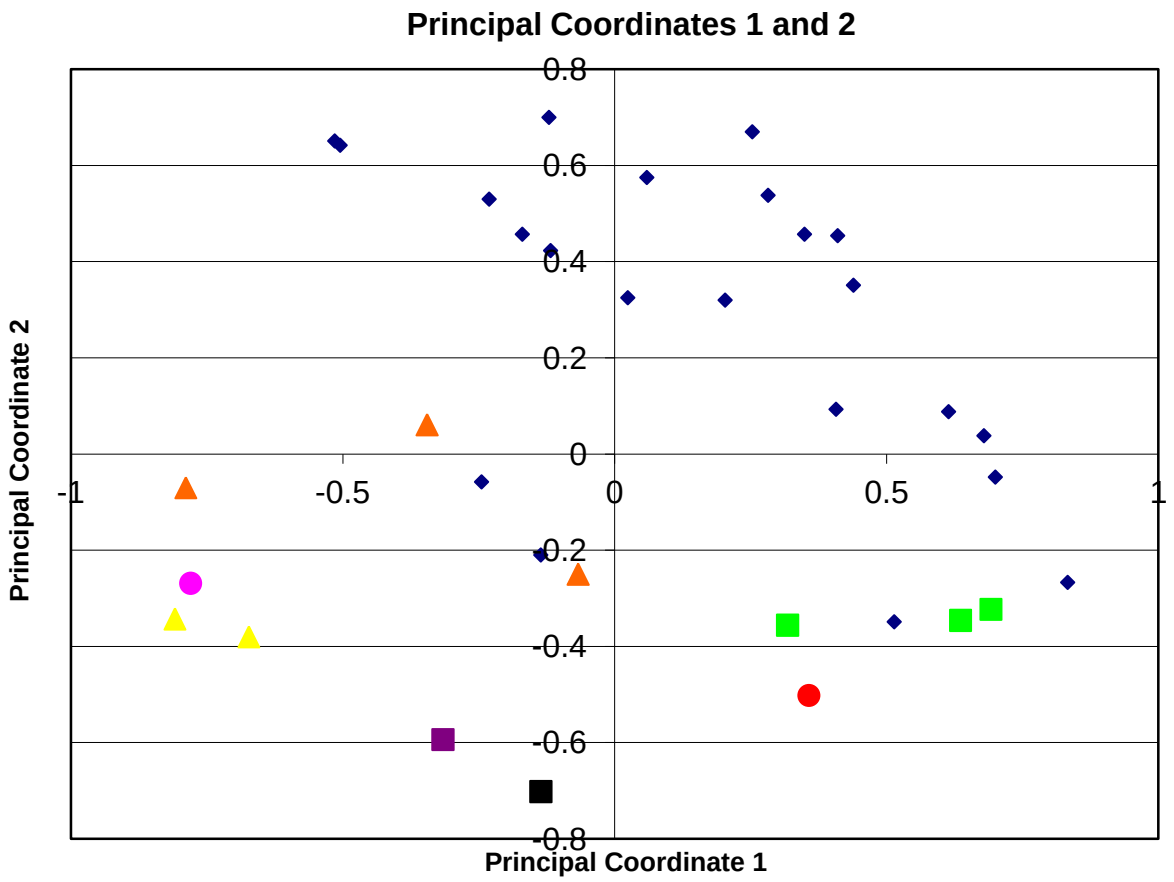

Figure 1: Principal coordinates 1 & 2; Herto (red circle), Skhul V (black square), Steinheim (purple square), Kabwe (pink circle), *Homo sapiens sapiens* (blue diamonds), Upper Paleolithic *Homo sapiens* (green squares), *Homo erectus* (yellow triangle), Neanderthals (orange triangles). Herto and UP*H.s.* lie within the range of variation for *H.s.s.* in principal coordinate 1 and outside the range of variation for *H.s.s.* in principal coordinate 2. Herto does not lie intermediate between Kabwe and more modern *H.s.* (i.e., Cro-Magnon 1, Predmosti 3 & 4, or Skhul V).

In principal coordinates one and three we can see that Herto falls well within the range of variation for the *Homo sapiens sapiens* sample as does the Upper Paleolithic *Homo sapiens* sample (Figure 2). Again, principal coordinate one is primarily controlled by neurocranial measurements, positively, and the size and shape of the middle to upper face, negatively (Table 2). Principal coordinate three is influenced by the parietal chord, orbital breadth, glabella-lambda length, and biorbital breadth, positively, and overall size of the neurocranium, negatively (Table 2). In these measurements Herto lies closer to the mean for *Homo sapiens sapiens* than the Upper Paleolithic *Homo sapiens* fossils (Figure 2). However, Herto, Skhul V, and all three Upper Paleolithic *Homo sapiens* fossils fall within the range of variation seen in our modern *Homo sapiens sapiens* sample. Unexpectedly, Steinheim and two of the three Neanderthals crania also fall within the range of variation for our modern *Homo sapiens sapiens* sample. This may relate to the inability of these variables for discerning between species or more pointedly sub-species. Again, Herto is not shown to be intermediate between Kabwe and anatomically modern *Homo sapiens*.

In the original analyses by White et al.'s (2003) their three-dimensional graph showed the Herto fossil was outside the range of variation for their *Homo sapiens sapiens* sample in all three

principal coordinates. This is likely due, in part, to the use of only neurocranial measurements by White et al. (2003), as well as our use of a different *Homo sapiens sapiens* sample. However, our analysis, which includes facial measurements, indicates that only in one coordinate is Herto outside the range of variation of our *Homo sapiens sapiens* sample (i.e., principal coordinate 2). This seemingly cloudy picture of the relationship among specimens in the original analyses was the initial reason that these new analyses were undertaken.

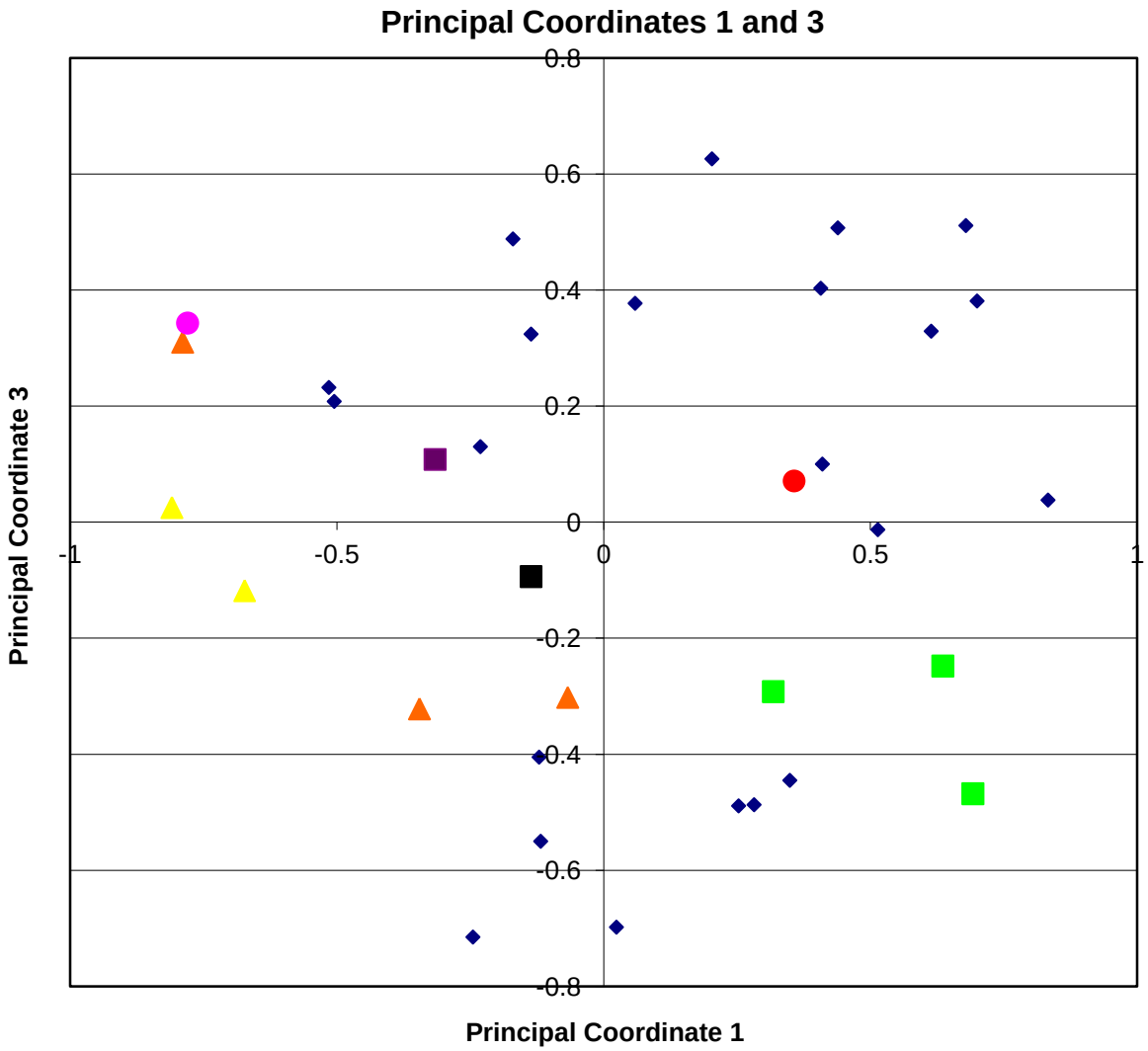

Figure 2: Principal coordinates 1 & 3; Herto (red circle), Skhul V (black square), Steinheim (purple square), Kabwe (pink circle), *Homo sapiens sapiens* (blue diamonds), Upper Paleolithic *Homo sapiens* (green squares), *Homo erectus* (yellow triangle), Neanderthals (orange triangles). Herto, as well as Steinheim, Skhul V, two Neanderthal crania, and the UP*H.s.* sample, lie within the range of variation for *H.s.s.* in principal coordinate 1 and 3. The Kabwe cranium, both *Homo erectus* fossil crania, and a Neanderthal fossil cranium lie outside the range of variation for our *H.s.s.* sample. Herto, is again, not intermediate between Kabwe and more modern *Homo sapiens*.

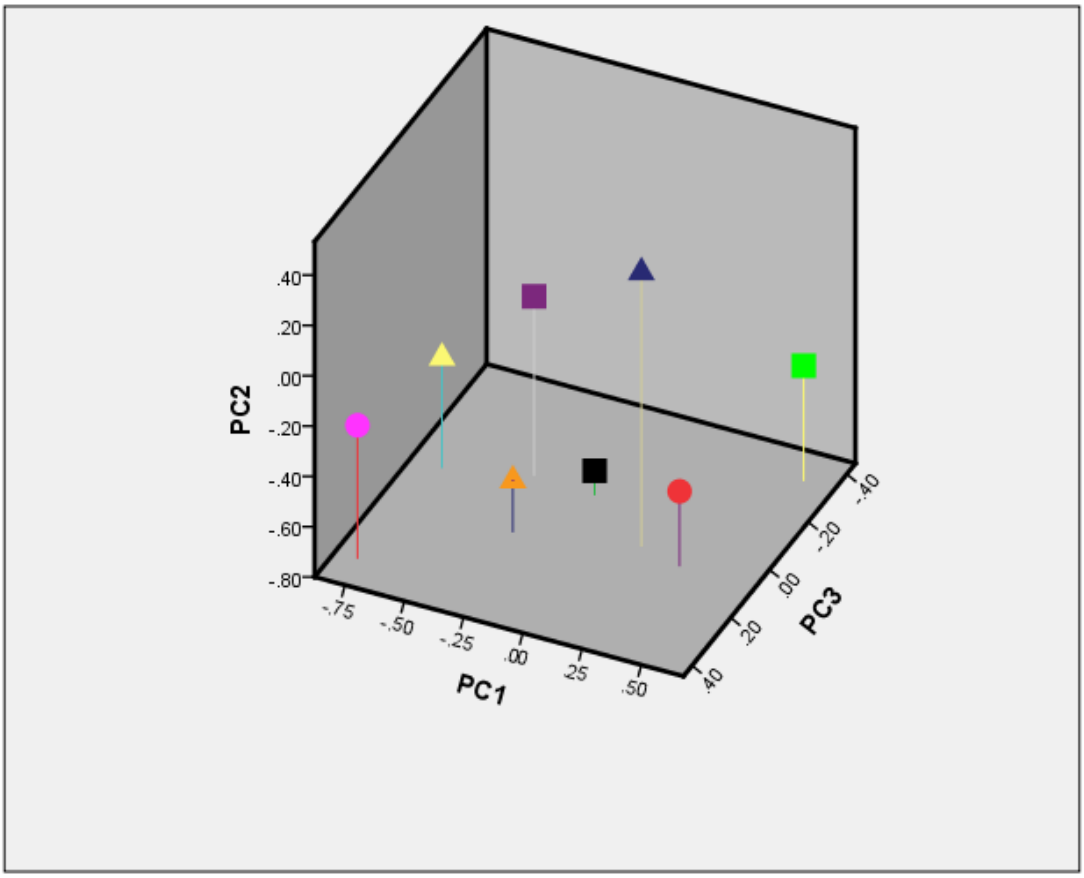

Figure 3: Principal coordinates 1 through 3, with means for the modern *Homo sapiens sapiens* (blue diamond), Upper Paleolithic *Homo sapiens* (green squares), *Homo erectus* (yellow triangle), and Neanderthals (orange triangles) samples, compared to individual scores for Herto (red circle), Skhul V (black square), Steinheim (purple square), and Kabwe (pink circle). In principal coordinates 1 through 3, paying attention to the scales, Herto lies closest to the mean for UP*H.s.* In principal coordinate 1 and 3 Herto and Skhul V are most similar to the mean for *H.s.s.* Here too, Herto is not intermediate between Kabwe and more modern *H.s.*

When all three of the principal coordinates are plotted utilizing the means for our Asian *Homo erectus*, Neanderthals, *Homo sapiens sapiens*, and our Upper Paleolithic *Homo sapiens* samples, as well as the individual measurements for Herto, Kabwe, Skhul V, and Steinheim a clearer picture of the relationship of these specimens is revealed. In Figure 3, it is clear that when principal coordinates one through three are examined in multidimensional hyperspace, paying close attention to the scale for each principal coordinate, that Herto is most similar to the Upper Paleolithic *Homo sapiens*, then Skhul V, and then our modern *Homo sapiens sapiens*, in that order. It also becomes clear that Herto does not lie intermediately between Kabwe and our modern *Homo sapiens sapiens* sample mean. Kabwe and the *Homo erectus* sample mean are considerably more distant from our modern *Homo sapiens sapiens* sample mean, than Herto.

When examining figure three, as well as these data from tables one and three, we can see that Herto is separated from the *Homo sapiens sapiens* sample mean primarily in principal coordinate two, which is driven by the wider biorbital breadth of the Herto fossil. Herto is also separated to a lesser degree from the Upper Paleolithic *Homo sapiens* sample mean in principal coordinate three which is driven by differences in parietal chord, positively, as well as maximum cranial breadth and maximum frontal breadth, negatively. Skhul V and Herto are also similar

with the majority of difference being in principal coordinate one, which is driven by the greater length of the parietal chord and nasion-prosthion, as well as the taller nasal height and orbital height in Herto. What is most interesting is that the Herto fossil lies slightly closer to the Upper Paleolithic *Homo sapiens* sample mean than to Skhul V. This could be due to the particular variables utilized or the larger Upper Paleolithic *Homo sapiens* sample size.

	PC 1	PC2	PC3
Modern *H.s.s.* mean	0.169318	0.29	0.038727
UP*H.s.* mean	0.548667	-0.34167	-0.336
Neanderthal mean	-0.40033	-0.08633	-0.10467
Skhul V	-0.136	-0.702	-0.094
Herto	0.357	-0.502	0.071
Steinheim	-0.316	-0.594	0.108
Kabwe	-0.78	-0.269	0.343
H erectus Mean	-0.741	-0.3615	-0.0465

Table 3: Principal coordinate 1 through 3 scores for our modern *H.s.s.* mean, UP*H.s.* mean, Neanderthal mean, Skhul V, Herto, Steinheim, Kabwe, and *Homo erectus* mean. These data are provided to clarify Figure 3 results.

The combined comparisons of principal coordinates one through three suggests that the Herto fossil is morphologically most similar to Upper Paleolithic *Homo sapiens* and Skhul V. The fact that the Herto fossil lies morphologically just outside the range of variation for only one of three principal coordinates for our *Homo sapiens sapiens* sample suggests that Herto has a close morphological affinity to both anatomically modern *Homo sapiens* (i.e., our Upper Paleolithic *Homo sapiens* sample) and fully modern *Homo sapiens sapiens*. We also find it noteworthy that Herto, Skhul V, the Upper Paleolithic *Homo sapiens* sample all cluster around the mean for the *Homo sapiens sapiens* sample (Figure 3).

Euclidean Distances

The individual Euclidean distances for Herto, Kabwe, and Skhul V were compared to the Euclidean Distance means for *Homo sapiens sapiens* and Upper Paleolithic *Homo sapiens* samples using the Paleontological Statistics (P.A.S.T.) program, in order to clarify the relationship between Herto, Kabwe, Skhul V and more modern members of our *Homo sapiens sapiens* and Upper Paleolithic *Homo sapiens* samples (Hammer et al. 2001). These analyses show that Herto is most similar to the Upper Paleolithic *Homo sapiens* sample and Skhul V, respectively (Table 4). Correspondingly, the Herto and Skhul V crania, as well as our Upper Paleolithic *Homo sapiens* sample mean are morphologically most similar to our modern *Homo sapiens sapiens* sample (Table 4). Kabwe is the most dissimilar of this sub-sample. These results fall in line with those of the principal coordinate data.

	H.s.s.	UP*H.s.*	Herto	Skhul V	Kabwe
H.s.s.	0	0.82664	0.81457	1.0464	1.1429
UP*H.s.*	0.82664	0	0.47759	0.81066	1.4939
Herto	0.81457	0.47759	0	0.55702	1.1921
Skhul V	1.0464	0.81066	0.55702	0	0.89061
Kabwe	1.1429	1.4939	1.1921	0.89061	0

Table 4: Euclidean Distances based on the mean principal coordinate data for our *Homo sapiens sapiens* and Upper Paleolithic *Homo sapiens*, as well as the individual principal coordinate data for Herto, Skhul V, and Kabwe. Herto and UP*H.s.* sample are the most similar to each other with Skhul V being slightly more distant. The *H.s.s.* sample is nearly equally distant to UP*H.s.* sample and Herto.

DISCUSSION

Our principal coordinate analyses show results similar to those of White et al. (2003) with three important exceptions that must be noted. First, White et al. (2003), states that the Herto (BOU-VP-16/1) specimen fell outside the range of variation in all three principal coordinates for their sample of fully modern *Homo sapiens.* Conversely, our principal coordinate analyses indicate that this Herto specimen falls just outside the range of variation for our *Homo sapiens sapiens* sample in only the second principal coordinate (Figure 1). This principal coordinate is primarily driven by orbital height and cranial capacity, positively, and biorbital breadth, negatively (Table 2). In principal coordinate two our Upper Paleolithic *Homo sapiens* sample is just inside the range of variation for our modern *Homo sapiens sapiens* sample. Furthermore, the UP*H.s.* crania lie between Herto and the vast majority of the *Homo sapiens sapiens* sample (Figure 1). However, in our analyses Herto lies within the range of variation for both principal coordinates one and three (Figure 2), in contrast to White et al. (2003). The first principal coordinate is primarily driven by the size of the neurocranium, positively, and the facial height, negatively (Table 2). The third principal coordinate loadings are primarily driven by parietal chord, positively, and breadth of the neurocranium, negatively (Table 2). In the first and third principal coordinates the Herto specimen and the Upper Paleolithic fossils lay within the range of variation for our *Homo sapiens sapiens* sample (Figure 2). These finding are most likely the result of the inclusion of facial measurements, which White et al. (2003) did not utilize, or differences in the *Homo sapiens sapiens* sample sizes.

Second, our principal coordinate results support the most fundamental findings of White et al. (2003) that the Herto fossil (BOU-VP-16/1) does appear to be a transitional form between archaic members of the genus *Homo* and later more modern forms of *Homo sapiens* (i.e., Skhul V and our Upper Paleolithic *Homo sapiens*). However, our data do not indicate that Herto is "intermediate" between Kabwe and more modern examples of *Homo sapiens,* as suggested by White et al. (2003). Herto is morphologically closest to our Upper Paleolithic *Homo sapiens* sample and Skhul V based on both the principal coordinate and Euclidean distance analyses. These results clearly imply that Herto is closer to more modern examples of *Homo sapiens* than the more archaic Kabwe specimen. We also agree with White et al. (2003) that this specimen, along with other discoveries in Africa, makes a strong case against any regional continuity with regards to the genesis of anatomically modern *Homo sapiens*. That it is not itself truly anatomically modern, as White et al. (2003) emphasized, is dependent on the realization that Skhul V is not anatomically modern (Stein and Rowe 2011; Corruccini, 1992).

Third, our analyses do not support or refute the statement by White et al. (2003) that this specimen is different enough to be classified as a new subspecies (i.e., *Homo sapiens idaltu*). The close morphological affinity to both Upper Paleolithic *Homo sapiens* and fully modern *Homo sapiens sapiens* implies that Herto is not different enough to warrant the development of a new sub-species. However, the fact that Steinheim and some of the Neanderthal fossils also fall within the range of variation for *Homo sapiens sapiens* suggests that these measurements are not enough to separate species, and especially sub-species, from each other. The ability of these analyses to separate species and potentially sub-species is also reliant on one's interpretation of the phylogenetic relationship between *Homo sapiens sapiens* and Neanderthals, as well as the acceptance that these traits are adequate for discrimination. If one posits that Neanderthals are a sub-species of *Homo sapiens*, then these results are not discriminatory enough to separate sub-species and therefore we cannot support the assertion of White et al. (2003) that Herto is a sub-species (i.e., *Homo sapiens idaltu)* Conversely, if one views Neanderthals as a separate species

then these results could suggest that Herto, Skhul V, and our Upper Paleolithic group could also be separate species. Due to the inclusion of some Neanderthal crania and Steinheim within the modern *Homo sapiens sapiens* range of variation, it is the opinion of these researchers that these traits are not adequate to define species or sub-species but they are useful tools for determining morphological similarity and dissimilarity between fossil crania.

The analyses reported here, along with other mounting evidence, suggest that anatomically modern *Homo sapiens* first began to evolve in Africa somewhere between 150,000 and 50,000 years ago. Mellars (2002) suggests that the evidence for a behavioral transition to anatomically modern *Homo sapiens* can also be seen in the African archaeological record based on changes in stone tool technology in the form of blades, new tool forms, new tool materials, compound tools, decorative items, long distance exchange networks, musical instruments, and ceremonial burials. Mellars (2002) suggests that increasing complexity in technology and cultural features developed gradually by 70,000 years ago. McBrearty and Brooks (2000) also discuss behavioral evidence for the evolution of *Homo sapiens sapiens* in Africa around 100,000 years ago, emphasizing evidence of bone-tool manufacturing from the Border cave site about 80,000 years ago and shell beads dating to over 100,000 years ago. Fossil evidence for the development of anatomically modern *Homo sapiens* has come from other sites in Africa, as well. Rightmire and Deacon (1991) state that the morphology of the Klaises River Mouth cave fossil samples falls within the range of variation for *Homo sapiens sapiens* prior to 60,000 years ago. Grine et al. (1998) also examined fossil remains from the Klaises River Mouth cave site and found the materials were a mix of archaic and modern *Homo sapiens* traits. Likewise, Bräuer and Singer (1996) stated that the Klaises River Mouth cave site *Homo sapiens* fossil remains had morphologies that were transitional between archaic *Homo sapiens* and anatomically modern *Homo sapiens*.

CONCLUSION

The overall close morphological affinities between Herto the Upper Paleolithic group, and Skhul V suggests that the morphology of anatomically modern *Homo sapiens* was developing in East Africa before 150,000 years ago and had spread into the Levant by 80,000 years ago. The fact that Herto lies morphologically between the East African archaic *Homo sapiens* (i.e., Kabwe specimen) and more modern *Homo sapiens* (i.e., Skhul V, Cro-Magnon 1, and Saccopastore 1 & 2) implies that Herto is at least a transitional specimen. However, Herto's morphological similarity to our modern *Homo sapiens sapiens* samples, contrasted against its apparent greater distance from Kabwe, suggests that Herto is not intermediate between Kabwe and *Homo sapiens sapiens* as suggested by White et al. (2003). We also cannot state that Herto lies outside the range of variation for fully modern *Homo sapiens sapiens*, as White et al. (2003) did. In many respects Herto is within the range of variation for fully modern *Homo sapiens sapiens* when both cranial and facial measurements are utilized. This does suggest the potential that Herto is not so unique to classify it as a new sub-species. However, the inclusion of some Neanderthal fossils and the Steinheim fossil, which also lie within the range of variation for *Homo sapiens sapiens*, further clouds the ability of these traits to separate species and sub-species. Nevertheless, we can agree with White et al. (2003) that Herto does present strong evidence of "sapienization" taking place in Africa between 200,000 and 100,000 years ago. This evidence, when added to mounting archaeological, paleoanthropological, and genetic data, does not support the "Multi-Regional Continuity Model".

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