

# Population Affinities of the Jebel Sahaba Skeletal Sample: Limb Proportion Evidence

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**ABSTRACT** The Lower Nubian Epipaleolithic site of Jebel Sahaba (Sudan) was discovered in 1962. From 1962 to 1966, a total of 58 intentionally buried skeletons were uncovered at the site. Diagnostic microliths indicative of the Qadan industry as well as the site's geology suggest an age of 14–12 ka for these burials. In this study, the body proportions of the Jebel Sahaba sample are compared with those of a large (max  $N=731$ ) sample of recent human skeletons from Europe, Africa and circumpolar North America, as well as to terminal Pleistocene 'Iberomaurusian' skeletons from the Algerian sites of Afalou-Bou-Rhummel and the later Capsian-associated Ain Dokhara specimen, as well as Natufian skeletons from the southern Levantine site of El Wad.

Bivariate analyses distinguish Jebel Sahaba from European and circumpolar samples, but do not tend to segregate them from recent North or sub-Saharan African samples. Multivariate analyses (principal components analysis, principal coordinates analysis with minimum spanning tree and neighbour-joining cluster analyses) indicate that the body shape of the Jebel Sahaba humans is most similar to that of recent sub-Saharan Africans and different from that of either the Levantine Natufians or the northwest African 'Iberomaurusian' samples. Importantly, these results corroborate those of both Irish and Franciscus, who, using dental, oral and nasal morphology, found that Jebel Sahaba was most similar to recent sub-Saharan Africans and morphologically distinct from their penecontemporaries in other parts of North Africa or the groups that succeed them in Nubia. Copyright © 2013 John Wiley & Sons, Ltd.

*Key words:* body shape; climatic adaptation; late Pleistocene

## Introduction

The northern Sudanese (Lower Nubian) Epipaleolithic burial site 117, named for the nearby hill of Jebel Sahaba, was first discovered in January 1962 by Roland Paepe and Jean Guichard during archaeological survey of areas to be flooded by the rising waters behind the Aswan High Dam (Wendorf, 1968). The site itself was located about 1 km from the east bank of the Nile, ~3 km north of the town of Wadi Halfa, at an elevation of roughly 160 m above sea level. This area is now flooded except when water levels in Lake Nasser/Nubia are low. During the 1962 field season, Paepe and Guichard found the remains of three adults and one 6-year-old child. Fred Wendorf then visited the site in 1965, where his team began extensive excavations. In late 1965, a Finnish team resumed work at the site,

recovering three burials (Wendorf, 1968). Finally, in October 1966, Anthony Marks began work at the site, uncovering eight more burials for a total of 58 skeletons (Wendorf, 1968). Although radiocarbon dates for the material were unavailable, the artefacts (including diagnostic microliths suggestive of the Qadan industry; see succeeding discussions) as well as the site's geology suggest an age of 14 000–12 000 BP for the burials (Wendorf, 1968).

The burials at Jebel Sahaba were both single interments and multiple burials of two to four (and possibly eight) individuals, all in shallow grave pits (Wendorf, 1968). These were obviously intentional burials, with bodies preferentially flexed, lying on their left sides, their long axes north to south, heads to the east facing south and with face in hands. Also, most of the burials were covered by sandstone slabs, making the task of their discovery easier (Wendorf, 1968). Perhaps the most noteworthy aspect of the Jebel Sahaba burials was the finding that most, if not all, of the individuals had died quite violent deaths. Six ulnae and one radius showed signs of parry fractures presumably acquired

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when warding off a blow (Anderson, 1968). Wendorf (1968) counted some 110 artefacts as being in direct association with the burials; most of these were points or apparent barbs and were found in positions such that they had obviously penetrated the body in the form of projectiles or spears. Favoured targets included the vertebral column and thoracic cavity, but two stone implements were still imbedded in the sphenoids of their victims, their positions indicating that they had entered the cranium from beneath the mandible (Wendorf, 1968). Additionally, eight of the individuals showed evidence of cut marks on relatively fresh bone with no evidence of bony reaction, suggestive of perimortem infliction (Anderson, 1968).

The fact that so many of the tools associated with the burial sample were projectile weapons made assignment of the Jebel Sahaba artefacts to a prehistoric Nubian industry somewhat more difficult, as the tools represented only a limited part of the total lithic assemblage. However, there are some clues linking the tools to the Qadan industry (ca. 15 000–7000 BP; Wendorf, 1968). For example, the majority of tools were made on flakes, with limited use of the Levallois technique, with some emphasis on backed and truncated pieces (Wendorf, 1968). Perhaps the most diagnostic tool found at the site was a single lunate, a tool that distinguishes the Qadan from the earlier Germaian industry. This lunate tool, if not intrusive, would indicate that the burials are later than 15 ka, the time when such tools first appear in the region (Wendorf, 1968). Overall, the assemblage is said to be most similar to that from the nearby ANE-1 site (Wendorf, 1968). As Wendorf (1968) noted, however, the Qadan tools were only clearly used by the *enemies* of the buried dead at Jebel Sahaba, and there is unfortunately no means by which one can be certain that the site 117 individuals were using the same technology.

The late James Anderson (1968) wrote the first anatomical description of the Jebel Sahaba skeletal remains. Anderson was interested, as are many biological anthropologists, in the populational affinities of his sample and was critical of the typological approach taken by many of his contemporaries into such questions. His report is therefore cautious in its assessment of group affinities, while quite thorough in its comparison of the remains to other fossil and recent human samples. First, he compared the sample with the so-called Cro-Magnons from the European Upper Palaeolithic sites of Combe Capelle and the Grimaldi Caves. A more important comparison was made between Jebel Sahaba and the remains from the nearby (and presumably contemporary) 'Colorado' Wadi Halfa remains. The sample was also compared with

somewhat more recent (Iberomaurusian) skeletons from Northwest Africa (the Maghreb), including, for example, the well-known Afalou-Bou-Rhummel and Taforalt (Grotte des Pigeons) specimens (Balout, 1955a), as well as to historic period Egyptian and Sudanese Nubians. He also compared the sample with late Pleistocene skeletons from East and Southern Africa.

Anderson concluded that the Jebel Sahaba skeletons were, as a group, quite homogeneous and that morphologically they were most similar to their presumed contemporaries from across the river at Wadi Halfa. Yet he also noted that they shared certain features with the Cro-Magnons, particularly with regard to cranial superstructures. However, he found that features more prone to show environmental effects (whether phenotypically plastic or otherwise) separated the tropical Jebel Sahaba skeletons from their penecontemporaries at higher latitudes. He could not find any evidence of morphological/genetic links between Jebel Sahaba and the late Pleistocene remains from East and Southern Africa (which were admittedly poorly preserved), but he did note a strong similarity between the sample and the Maghreb Mesolithic 'Mechtoid' material. Anderson (1968) used the term Mechtoid to refer to robustly built skeletons from the Maghreb, most notably from the site of Mechta-el-Arbi (from whence the name comes), and also from other Iberomaurusian sites in the region such as Afalou (Afalou-Bou-Rhummel) and Taforalt<sup>1</sup>. Also, although the Jebel Sahaba crania were more massively built and their faces broader and more prognathic than those of recent Nubians, Anderson argued for the existence of some traits indicative of microevolutionary continuity between Jebel Sahaba and much more recent skeletons from Nubia. In particular, the two groups exhibited a high degree of overlap in cranial measurements, both had a high percentage of occipital buns and gonial eversion, and neither group exhibited bregmatic bone or Ossa Incae (Anderson, 1968; p. 1030).

In contrast, Irish and Turner (1990) and Irish (2000, 2005) noted that late Pleistocene Nubians (and in particular the Jebel Sahaba skeletons) were as a group quite different from more recent Nubians for dental discrete traits, yet shared great phenetic affinity with recent West African populations. For example, Irish and Turner (1990) found that the mean measure of divergence, or MMD, between Pleistocene Nubians and Christian period Nubians was 0.379, whereas the MMD between Pleistocene Nubians and recent West

<sup>1</sup> The term Mechtoid typically excludes skeletal remains from the Maghreb associated with the Capsian industry, an industry slightly later in time than the Iberomaurusian. These skeletons are generally more gracile and are thought by some researchers to represent a different population (e.g. Camps, 1974; Dutour, 1995; but see Lubell *et al.*, 1984; Irish, 2000).

Africans was only 0.04. Counter to Anderson's (1968) argument, then, Irish and Turner (1990) argued for some degree of genetic discontinuity between Pleistocene and Holocene Nubians, with the former being more similar to modern-day West Africans, whereas the latter were more similar to recent North Africans and Europeans.

Irish (2000, 2005) found that late Pleistocene Nubians (and especially the Jebel Sahaba sample) are wholly dissimilar to Iberomaurusian populations from the Maghreb. He pointed out that despite the typological similarities in their cultural traditions (Iberomaurusian vs. Qadan), that dentally the two populations are easily distinguished. In fact, late Pleistocene Nubians (Jebel Sahaba) were the extreme outlier in a comparison of Pleistocene and Holocene North African groups (Irish, 2000, 2005). Irish (2000) also discovered discontinuity among the Mechtoid groups, whom others (Anderson, 1968; Greene & Armelagos, 1972; Dutour, 1995; Lahr & Arensburg, 1995) had previously argued were largely homogeneous. Specifically, whereas Afalou specimens could serve as an outgroup to a North African cluster of all but the late Pleistocene Nubians, the Tavoralt specimens shared closest phenetic affinities to a sample of Punic and/or Roman era Carthaginians, a presumed immigrant population from Western Asia.

These earlier studies are a good starting point for the current research. Armed with a large comparative data set, the current study reinvestigates the morphological/population affinities of the Jebel Sahaba sample from a postcranial perspective. In this, osteological data reflective of body proportions have been chosen for analysis. Although subject to selection and/or malnutrition, body proportions nonetheless show a sizeable genetic component and have been shown to take tens of thousands of years to alter in response to climatic selection (Holliday, 1997, 1999). Thus, body proportions have been used in the past to elucidate phylogenetic

relationships over evolutionarily short periods among late Pleistocene fossil hominids (Trinkaus, 1981; Holliday, 1997, 2000), operating under the assumption that phenetic similarities in these features are reflective of genetic affinities (see also Irish, 1998). In this paper, the Jebel Sahaba sample is compared with relevant penecontemporary fossils from Africa, the Levant and Europe, as well as to more recent humans from the Western Old World and circumpolar North America. Specifically, two hypotheses are tested, which are derived at least in part from Irish and Turner (1990) and Irish (2000, 2005). First, that the Jebel Sahaba sample share closest morphological affinity with recent sub-Saharan Africans and, second, that they are more similar in an overall phenetic sense to recent sub-Saharan Africans than they are to the penecontemporary Mesolithic samples from the Maghreb (including both Iberomaurusian- and Capsian-associated skeletons). Because body proportions are being investigated, ossuary samples, where bodies have been disarticulated prior to burial (such as Tavoralt or Grotte des Pigeons), are not included in the analyses.

## Materials and methods

The late Pleistocene–early Holocene samples studied, their archaeological associations, associated radiometric dates and where they are currently housed are found in Table 1. Included in the fossil sample are specimens from Nubia, northwestern Africa (the Maghreb) and the Levant. These samples date to the period from around the terminal Pleistocene into the earliest Holocene. In addition to the fossil samples, recent human skeletal samples are also included. These comparative samples are listed in Table 2 and are described in more detail elsewhere (Holliday, 1995; Holliday and Hilton, 2010). The samples are all younger than 4000

Table 1. Late Pleistocene–early Holocene samples used in the analyses

Sample	<i>n</i>	Archaeological associations	Date	Location
Afalou-Bou-Rhummel	5	Ibero-Marusian/Oranian <sup>a</sup>	Late Tardiglacial/early Holocene <sup>b</sup>	IPH
Ain Dokhara	1	Capsian <sup>c</sup>	Early Holocene <sup>c</sup>	IPH
El Wad	5	Natufian <sup>d</sup>	Early Holocene <sup>e</sup>	PMH
Jebel Sahaba	11	Qadan <sup>f</sup>	ca. 13 ka <sup>f</sup>	BM

IPH, Institut de Paléontologie Humaine, Paris; PMH, Peabody Museum, Harvard University, Cambridge, MA; BM, The Natural History Museum, London.

<sup>a</sup>Arambourg (1934).

<sup>b</sup>Oakley *et al.* (1977).

<sup>c</sup>Balout (1955a).

<sup>d</sup>Garrod and Bate (1937).

<sup>e</sup>Howell (1959).

<sup>f</sup>Wendorf (1968).

Table 2. Recent human samples used in the analyses

Sample	<i>n</i>	Period	Location
Circumpolar			
Koniag	21	Late 19th century AD?	SI
Ipiutak	45	100 BC–500 AD	AMNH
Tigara	116	1200–1500 AD	AMNH
Europe			
Bohemian	49	950–1050 AD	PMH
Bosnian	79	Before 1468 AD	PMH
French	32	Early medieval	HRT
German	31	8th to 15th centuries AD	UTT
Norse	23	10th century AD	BM
Romano-British	52	4th century AD	BM
North Africa			
Egypt	70	Predynastic to Middle kingdom	PMH
Nubian	24	4th to 7th centuries AD	DCC
Sudanese (Kerma)	50	3700–3500 BC	DCC
Sub-Saharan Africa			
East Africa	46	Mid-20th century AD	MUU, KNM
Pygmy	10	19th to 20th centuries AD	UG, ISN,
San	8	19th century AD?	BM
West Africa	21	19th century AD?	BM, MH

SI, Smithsonian Institution, Washington DC (since repatriated); AMNH, American Museum of Natural History, New York; PMH, Peabody Museum, Harvard University, Cambridge, MA; HRT, Hôpital Rangueil, Toulouse; UTT, University of Tübingen, Tübingen; BM, The Natural History Museum, London; DCC, Duckworth Collection, Cambridge University, Cambridge; MUU, Makerere University, Kampala; KNM, Kenya National Museums, Nairobi; UG, University of Geneva, Geneva; ISN, Institut Royale des Sciences Naturelles, Brussels; MH, Musée de L'Homme, Paris.

years BP and come from North Africa (including Nubia), sub-Saharan Africa, Europe, and the circumpolar region of North America. This sample provides a broad-cross section of populations from multiple climatic zones to whom the Jebel Sahaba skeletons are compared.

Five postcranial measurements are included in the analysis: femoral antero-posterior head diameter (M-19; FHAP), femoral bicondylar length (M-2; FL), tibial maximum length (M-1; TL), humeral maximum length (M-1; HL) and radius maximum length (M-1; RL). These are all standard osteometrics and provide a good measure of body size and proportions, as all four limb segments are represented and as femoral head diameter is highly correlated with body mass (Jungers, 1988, 1990). All measurements were preserved in each of the individuals included in the recent human sample. However, some of these measurements, particularly those from the somewhat fragmentary Jebel Sahaba sample, were not preserved in the fossils and thus had to be estimated from incomplete bones. This was accomplished via ordinary least-squares (OLS) regression equations of total bone length regressed on partial length for a complete series ( $n = 30$ ) of recent Euroamericans from the Maxwell Museum of Anthropology at the University of New Mexico. The predictive equations used, the resulting limb bone lengths, their standard errors and 95% confidence intervals are presented in Table 3.

It was decided *a priori* that a bone length estimated in such a manner would only be used if its standard error

of the estimate was lower than 3% of the estimated measurement itself. As seen in Table 3, nine limb bone lengths for eight Jebel Sahaba individuals and one individual from Afalou were estimated using five regression equations. The standard error of the estimate for these predictions indicates that the predicted bone lengths are reliable; the standard error is on average 1.11% of the predicted total limb length, within a narrow range of 0.67–1.4%.

The postcranial/body shape affinities of the Jebel Sahaba skeletal sample were elucidated via three different methods. First, simple bivariate analyses of selected limb bone lengths (distal limb segments are used because they show greater geographic variance than do proximal limb segments) regressed on femoral head diameter were employed as a means of assessing body linearity relative to body size. This has an added benefit in that it includes more fossils than can be analysed with multivariate procedures, because of incomplete preservation. Multivariate analyses begin with the computation of 'log shape' variables *sensu* Darroch and Mosimann (1985) for the all five measurements in the postcranial data set. Shape variables computed this way remove an isometric size component and thus provide a clearer picture of shape differences between individuals and/or samples. The log shape variables were then subjected to principal components analysis (PCA) using NCSS 2007 (NCSS, LLC, Kaysville, UT, USA) (Hintze, 2007). Combined-sex means of these



Table 3. Results of equations used to predict long bone length in the fossil sample

Specimen	$\hat{Y}$	SE $\hat{Y}$	% of $\hat{Y}$	95% CL
Regression no. 1: $\hat{Y} = 1.068x + 1.325$ , $r^2 = 0.984$ (regression of femoral bicondylar length on length between proximal margin of head and proximal margin of lateral epicondyle)				
Jebel Sahaba 117-22	416.0	3.911	0.94	408.0–424.0
Jebel Sahaba 117-40	492.7	4.044	0.82	484.4–501.0
Regression no. 2: $\hat{Y} = 1.031x + 28.971$ , $r^2 = 0.959$ (regression of maximum tibial length on distance between distal medial malleolus and midpoint of tibial tuberosity)				
Afalou 25	392.0	5.475	1.40	380.8–403.2
Jebel Sahaba 117-6	395.0	5.533	1.40	383.7–406.3
Regression no. 3: $\hat{Y} = 1.017x + 31.312$ , $r^2 = 0.978$ (regression of maximum tibial length on distance between distal articular surface and proximal margin of tibial tuberosity)				
Jebel Sahaba 117-18	391.4	4.106	1.05	383.0–399.8
Regression no. 4: $\hat{Y} = 0.961x + 21.413$ , $r^2 = 0.990$ (regression of maximum tibial length on distance between proximal intercondylar eminence and distal articular surface at midline)				
Jebel Sahaba 117-29	413.0	2.775	0.67	407.3–418.7
Regression no. 5: $\hat{Y} = 1.015x + 30.459$ , $r^2 = 0.971$ (regression of maximum humeral length on distance between surgical neck and distal trochlea)				
Jebel Sahaba 117-18	342.1	4.194	1.23	333.5–350.7
Jebel Sahaba 117-29	355.3	4.298	1.21	346.5–364.1
Jebel Sahaba 117-39	336.0	4.159	1.24	327.5–344.5

shape variables were next computed for each of the fossil and recent human samples (with the exception of the single specimen from Ain Dokhara) and were then used to generate a Euclidean distance matrix, which was subjected to two different multivariate cluster analyses using a PC version of NTSYS (Exeter Software, Setauket, NY, USA) (Rohlf, 1990). The first of these methods was a principal coordinates analysis with a minimum spanning tree fit to the mean coordinates. The second is a dendrogram generated via the neighbour-joining (NJ) method. Results of these clustering algorithms were compared for consistency.

## Results

Analyses begin with the scatter plot of radius length on femoral head diameter, presented in Figure 1. The regression lines shown are OLS lines for regional samples of recent humans. Note that despite much overlap among recent human samples in bivariate space, there is nonetheless a clear clinal pattern in which the sub-Saharan Africans tend to have the longest radii relative to their femoral head size, followed by the North Africans who have the next longest radii. In contrast, the North American circumpolar populations tend to have the shortest radii relative to their femoral head size, whereas the Europeans have radii that are on average longer than those of the circumpolar populations and somewhat shorter on average than the North Africans.

The Jebel Sahaba sample, indicated by stars, tend to have longer radii relative to the size of their femoral heads than do any of the other fossil groups. Relative to the recent human groups, the Jebel Sahaba specimens tend to cluster about the sub-Saharan African regression line. Four of the eight Jebel Sahaba specimens fall above the recent sub-Saharan African line (117-10, 117-26, 117-28 and 117-40), whereas one specimen

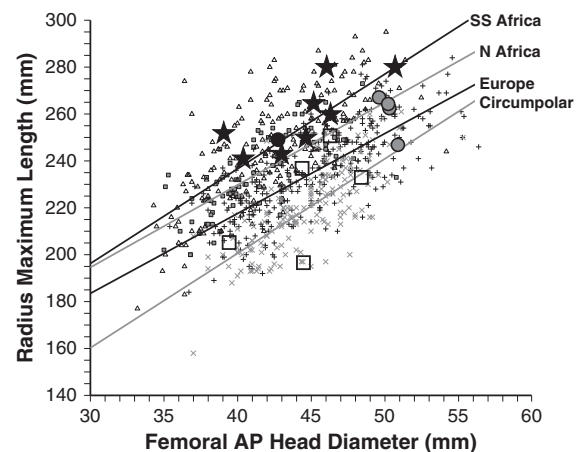


Figure 1. Scatter plot of radius length regressed on femoral head diameter, with ordinary least-square regression lines for the recent human groups indicated, by region. Recent humans: grey x's = circumpolar; black crosses = European and European diaspora; small grey squares = North Africans; small open triangles = sub-Saharan Africans and sub-Saharan African diaspora. Fossils: stars = Jebel Sahaba; black circle = Ain Dokhara 1; grey circles = Afalou; large open squares = El Wad Natufians.

falls on the line (117-29). Three Jebel Sahaba individuals (117-19, 117-22 and 117-39) fall below the recent sub-Saharan African OLS line, but all the Jebel Sahaba sample fall above the recent North African OLS line. Note that the Afalou specimens (the grey circles) all fall below the recent sub-Saharan African OLS line, with one individual (no. 28) falling below the recent European regression line and directly on the circumpolar line. Ain Dokhara 1 (the black circle), an early Holocene, Capsian-associated skeleton from Algeria (Balout 1955b), falls just above the recent sub-Saharan African OLS line. All five of the Natufian individuals from El Wad, Israel (the open squares), fall below the recent North African OLS line, and three of the five fall below the recent European regression line.

A similar, if less marked, clinal pattern is evident in the scatter plot of tibial length on femoral head size (Figure 2). Once again, the recent humans show a clinal pattern, with sub-Saharan Africans on average having the longest tibiae and circumpolar individuals possessing the shortest. As with the previous analysis, the North Africans are intermediate between the sub-Saharan Africans and the Europeans, whereas the Europeans tend toward longer tibiae than the Inuits. As a group, the Jebel Sahaba sample (the stars) tend to have longer tibiae for any given femoral head size than do the other fossil groups. Four of the eight Jebel Sahaba individuals (117-1, 117-6, 117-10 and 117-26) fall above the recent sub-Saharan African OLS line, with a fifth individual (117-19) falling directly on it. Three Jebel Sahaba individuals (117-18, 117-28 and 117-39) fall below the sub-Saharan OLS line. Of these,

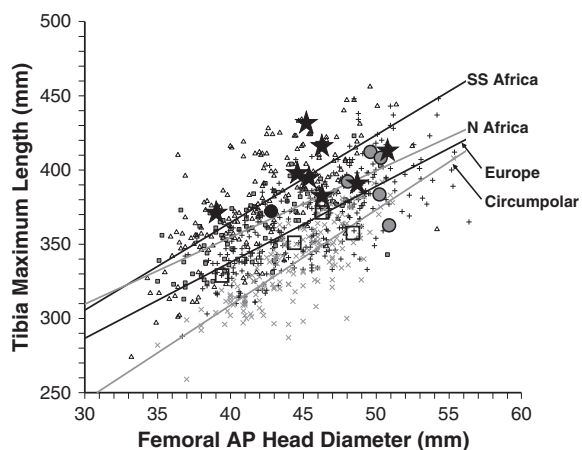


Figure 2. Scatter plot of tibial length regressed on femoral head diameter, with ordinary least-square regression lines for the recent human groups indicated, by region. Recent humans: grey x's = circumpolar; black crosses = European and European diaspora; small grey squares = North Africans; small open triangles = sub-Saharan Africans and sub-Saharan African diaspora. Fossils: stars = Jebel Sahaba; black circle = Ain Dokhara 1; grey circles = Afalou; large open squares = El Wad Natufians.

117-28 lies above the recent North African OLS line, 117-39 falls directly on it and 117-18 falls just below it.

In contrast, none of the Afalou skeletons (the grey circles) falls above the sub-Saharan African line; rather, they tend to cluster about the North African and European lines. Afalou 28 actually falls below the recent circumpolar human regression line for the tibial length: femoral head size relationship. Ain Dokhara 1 (the black circle) falls just above the North African and just below the sub-Saharan African OLS lines. The El Wad Natufians (the open squares) all cluster on or below the European regression line.

Multivariate analyses begin with PCA based on the variance–covariance matrix (VCM) of a data set that includes the natural logarithms of all the measurements listed in the Materials and methods: femoral head A-P diameter and femoral, humeral, tibial and radial lengths (and shape variables were calculated from these measurements as described in the Materials and methods). The reduction in total variance (i.e. the sum of all eigenvalues) from the VCM of the log-transformed measurements to that of the log shape measurements indicate that ~18.5% of the total variance is attributable to shape. The results of the PCA of the log shape variables are presented in Table 4. Combined, the first and second principal components account for 84.9% of the total shape variance. The first principal component accounts for 72.3% of the variance and primarily contrasts femoral head size with tibial and radial length. The second principal component accounts for 12.6% of the variance and contrasts radius length with femoral length. These differences are best seen visually in Figure 3, which is a plot of the PC scores for the individual fossil specimens and male and female means for the recent human samples. The scores along the first principal axis contrast those individuals and sample means on the left, who tend to have smaller femoral heads and longer radial and tibial lengths, with those individuals and sample means on the right, who tend

Table 4. Principal components of log shape variables: fossil and recent humans

	Eigenvector coefficient	
	I	II
FHAP	0.864383	0.113548
FL	-0.101974	-0.458467
TL	-0.340695	-0.369377
HL	-0.074020	-0.081809
RL	-0.347694	0.796105
Eigenvalue	0.005057	0.000880
% total variance	72.3	12.6

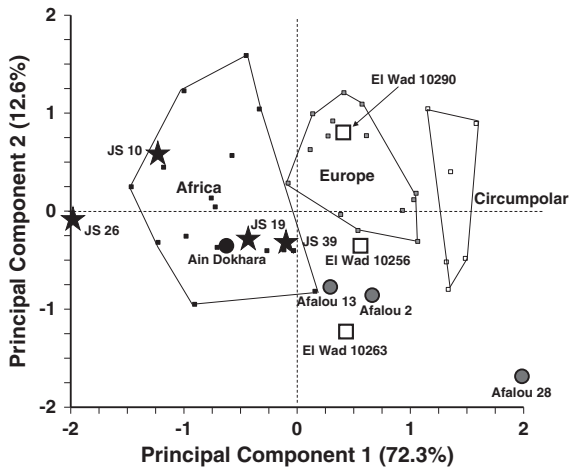


Figure 3. Scatter plot of principal component 2 on principal component 1, for full postcranial variable set, log shape data. Male and female means for the recent human samples are indicated by small squares. Lines have been drawn about the margins of the geographic regions to aid in the interpretation of the plot. Jebel Sahaba specimens are represented by stars, Afalou specimens by grey circles, El Wad Natufians by open squares and Ain Dokhara by black circle.

to have larger femoral heads and shorter tibial and radial lengths. This principal axis is best interpreted as a climatic adaptation gradient, with those individuals on the left evincing a heat-adapted postcranial morphology, whereas those on the right evince a more cold-adapted morphology. The second principal component does not distinguish the groups from each other. All of the Jebel Sahaba specimens lie at the heat-adapted end of the spectrum, and all but one individual

(117-26, who is perhaps 'extreme' in its heat adaptation) fall within the scatter of recent African means. Although not shown on the plot, the recent North African sample falls almost completely within the right side of the recent sub-Saharan African scatter, with one Jebel Sahaba specimen (117-39) falling within the range of both the recent North and sub-Saharan African sample means, a second (117-19) falling just outside the range of the North African sample means (but also within the range of the sub-Saharan Africans), whereas a third individual (117-10) falls outside of the North African range and just within the sub-Saharan African range. The Ain Dokhara specimen also falls within the scatter of recent African means. In contrast, none of the Afalou specimens, nor of the El Wad Natufian specimens, falls within the African scatter, and all lie toward the more cold-adapted end of the scatter. As was the case with the bivariate analyses, among the prehistoric skeletons, Afalou 28 looks the most extreme in its cold-adapted morphology, and note that this specimen was recovered some 2 m below the other human remains at the site (see succeeding discussions).

Cluster analyses are based on group means computed as the sum of the female mean and the male mean divided by 2. For the Jebel Sahaba sample, the mean was computed using the female 117-26 and the males 117-10, 117-19 and 117-39, as these are the only specimens who preserve all of the variables included in the analyses. The principal coordinates plot based on the five postcranial shape variables and its associated minimum spanning tree are shown in Figure 4. Recent

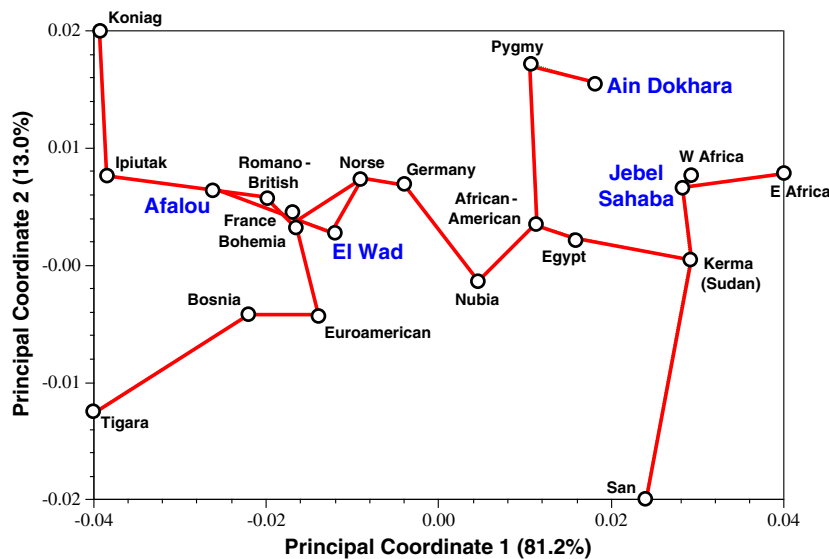


Figure 4. Plot of principal coordinate 2 on principal coordinate 1 with minimum spanning tree, fossil and recent human means (and a single individual for Ain Dokhara), based on the full postcranial variable set, log shape data. This figure is available in colour online at [wileyonlinelibrary.com/journal/oa](http://wileyonlinelibrary.com/journal/oa).

African groups tend to cluster together on the right side of the plot, whereas recent Europeans and circumpolar groups tend to cluster together on the left. Note that the Jebel Sahaba sample shares extremely close phenetic affinity with the recent West Africans, then is connected by two relatively short branches to the Sudanese from the site of Kerma and the East Africans, respectively. The Sudanese are then connected via one medium-length branch to the Egyptians and by a much longer branch to San. The Egyptians are connected via a short branch to recent African-Americans, who are then connected by one short branch to the recent Nubians and a second, much longer, branch to the African 'Pygmies'. The Pygmies themselves are connected via a short branch to the single Ain Dokhara individual. Among the higher latitude groups, the Germans are tied to the exclusively African cluster described earlier via a medium-length branch to the Nubian sample. Finally, the remainder of the European and circumpolar groups cluster together on the left-hand side of the plot, with the Afalou skeletons and El Wad Natufians clustering among them.

The NJ tree based on the five postcranial shape variables is displayed in Figure 5. The tree has two major branches, one with recent Africans and the second a combined recent European/circumpolar branch. Among the African groups, the Christian-era Nubians are an outlier to the remainder of the African groups, followed by the Pygmies and the Ain Dokhara individual. On the NJ tree, the Jebel Sahaba sample shares close phenetic affinity with recent East Africans, followed by the West Africans and Sudanese. They then sequentially join the San, Egyptians and

African-Americans. On the tree's other major branch, that is, among the recent European/circumpolar groups, the Germans are the outgroup, followed by the Norse and then the El Wad Natufians. Interestingly, the three circumpolar samples cluster together (albeit on long branches), and the fossils from Afalou are an outgroup to these circumpolar people.

## Discussion

The body proportions of the Jebel Sahaba sample are 'tropically adapted' with long distal limb segments relative to measures of their overall size. The current bivariate and multivariate results are somewhat consistent with the univariate results of Raxter (2011), who found that Jebel Sahaba male samples had significantly longer tibiae and humeri than other Nubian male samples. However, it is somewhat paradoxical that Raxter (2011) also found that the Jebel Sahaba sample tended to have lower brachial indices (generally reflective of less elongated antebrachia) than the other Egyptian and Nubian samples she analysed (for discussion of a different case of this seeming paradox, see Holliday (1999)).

The current results are also consistent with those of Irish (2000), who with dental data found that the Jebel Sahaba sample show closest phenetic affinity to contemporary sub-Saharan Africans. In the current body shape analyses, Jebel Sahaba either clusters most closely with recent East or West Africans, or with the 4000-year-old Kerma sample from Sudan, which, as an Upper Nubian site from south of the Third Cataract

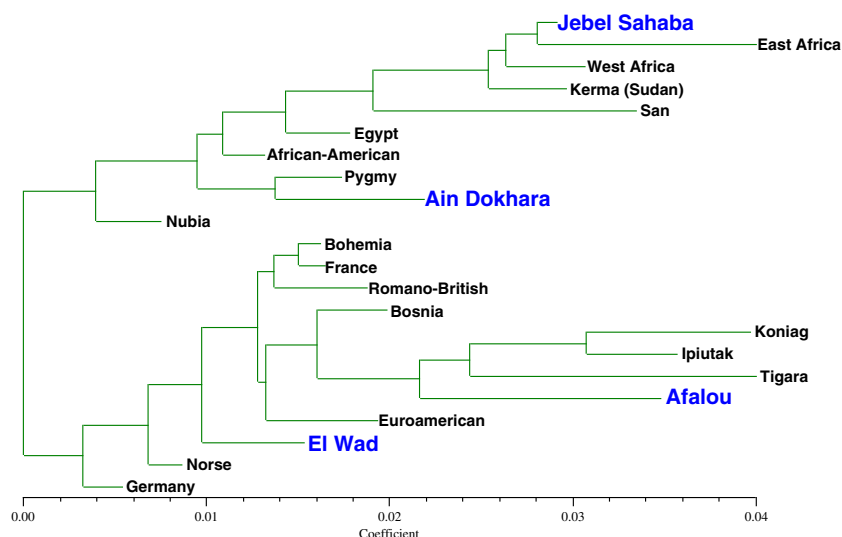


Figure 5. Neighbour-joining tree, fossil and recent human means (and a single individual for Ain Dokhara) for full postcranial variable set, log shape data. This figure is available in colour online at [wileyonlinelibrary.com/journal/oa](http://wileyonlinelibrary.com/journal/oa).



of the Nile, could be viewed as straddling the 'boundary' between North and sub-Saharan Africa (importantly, though, it is of note that the site of Kerma lies only ~260 straight-line km from Jebel Sahaba). As with the previous studies, the current findings suggest that the morphology of Jebel Sahaba is distinct from more recent Egyptian and Nubian samples, suggestive of a genetic discontinuity in the Nile Valley. One difference between the current study and these previous studies is that both Irish (2000, 2005) and Raxter (2011) found key morphological differences between the Jebel Sahaba and Kerma samples—differences that led Irish (2005) to argue for a genetic discontinuity between the late Pleistocene Nubians (as represented by Jebel Sahaba), the 'Kerma Classique' period skeletons (ca. 1750–1500 BC), and later Nubian samples. Specifically, he suspected that population replacement or genetic swamping occurred in Nubia sometime in the early Holocene (Irish, 2005). The current results are in agreement with this finding, with one subtle distinction. The current body shape results seem to place the time of the genetic discontinuity to a period subsequent to the mid-Holocene (i.e. after 4000 years ago), as opposed to the early Holocene. However, as with any complex evolutionary process, it was likely mosaic in nature and hence one should not expect all morphological characters to alter at the same rate or time.

The results of this study are also consistent with Robert Franciscus' work on nasal morphology (Franciscus, 1995, 2003). Assessing the morphology of the inferior nasal margin by using a modified version of De Villiers' (1968) scoring system, Franciscus (2003) reported that of the 21 Jebel Sahaba individuals whose nasal margins can be assessed, 13 (~62%) exhibit stage 7, whereas five (~24%) show a mixture of stages 3 and 7, and three other individuals (~14%) evince stage 3 alone. This is significant because stage 7 is the most common morphological configuration (reaching a frequency of 80%) among a large ( $n = 120$ ) sample of modern Bantu-speaking sub-Saharan Africans, but is completely absent in a sample of 140 Mediterranean and North African recent human crania, according to Franciscus (1995). In contrast, among the Iberomaurusian Late Pleistocene North Africans, only 1 of 19 (~5%) individuals from Afalou-Bou-Rhummel and only 2 of 19 (~11%) of the individuals at Taforal exhibit stage 7 (Franciscus, 2003).

Perhaps the most interesting finding of this study is the dramatic difference in body proportions between Jebel Sahaba and the penecontemporary late Pleistocene Algerian sample from Afalou-Bou-Rhummel. The former evince a tropically adapted morphology, whereas the latter show a more cold-adapted body shape. This

cold-adapted body form is most evident in Afalou 28, a male skeleton found buried 2 m below the other remains at the site, who was laid on his back with a child's cranium at his feet (Arambourg, 1934; Camps, 1974; Lubell *et al.*, 1984). Given the stratigraphic distance between this specimen and the other remains from Afalou-Bou-Rhummel, it is noteworthy that Afalou 28 is argued by many to be morphologically distinct from the other (later) humans from that site (Camps, 1974; Lubell *et al.*, 1984; but see Vaufrey, 1955).

There are multiple, not necessarily mutually exclusive, explanations as to why the Afalou and Jebel Sahaba humans are so different in their body shape. First, it is important to note that although both samples are North African, in terms of their environmental settings, the two sites are very different today and would also have been very different in the Pleistocene. Today, in the absence of human deforestation (and throughout the Pleistocene), the local environment at Afalou would be/have been characterised in a broad sense as Mediterranean, and in a narrower sense as subtropical dry forest to scrubland, depending on prevailing paleoclimatic conditions (Ruddiman *et al.* 1989; Trauth *et al.*, 2009; Larrasoana, 2012). In contrast, the local environment at Jebel Sahaba throughout most of the Holocene and Pleistocene would have been characterised as tropical desert, except during so-called Green Sahara periods, when the African summer monsoon would have reached as far north as 25°N. During such periods, the area near Jebel Sahaba would have been more savannah-like (Larrasoana, 2012). Thus, one might expect climatic selection at these two North African sites to be quite different.

Second, it is also of note that Afalou and Jebel Sahaba are separated by more than 2900 km, which would likely tend to limit gene flow between them, especially given lower population densities of humans in the Pleistocene. Gene flow between the sites would have been further constrained during expansions of the Sahara, limiting gene flow to the narrow Nile Valley up to the Mediterranean coast. In contrast, gene flow likely would have increased during the Green Sahara periods at ca. 215, 195, 170, 125, 100 and 80 ka (Larrasoana, 2012). Throughout the Pleistocene, then, during both expansions and retractions of the Sahara, gene flow would have been more or less continuous up the Nile corridor (albeit likely at lower levels than after the advent of agriculture, because of generally low population densities). For this reason, the Nile corridor is thought to have served as one of the main, if not the main, human 'gateway' into Eurasia (Larrasoana, 2012). One could therefore imagine that given its location in the Nile Valley, Jebel Sahaba would have

experienced relatively elevated levels of gene flow from sub-Saharan Africa throughout the Pleistocene—and such gene flow would not have been as marked at Afalou.

Thus, different climatic regimes as well as isolation-by-distance gene flow from sub-Saharan Africa could explain the difference in body shape evidenced between Afalou and Jebel Sahaba. One might be tempted to argue that the more tropical build of Ain Dokhara 1 suggests that humans associated with the Capsian industry reflect a later increase in gene flow and/or migration from sub-Saharan Africa, with the Capsians genetically distinct from the older 'Iberomaurusian' populations (an argument that has been made historically: Camps, 1974; Dutour, 1995; but see Lubell *et al.*, 1984; Irish, 2000). However, Ain Dokhara 1 is but a single specimen, so the body proportion data in this particular case are not sufficient to make this argument.

## Conclusions

The body shape of the terminal Pleistocene Jebel Sahaba population is tropical-adapted, with elongated limbs, especially in the distal segments, and is most similar to living sub-Saharan Africans and less similar to late Pleistocene and Holocene North Africans (including Egyptians and Nubians). The sample's body shape likely reflects elevated gene flow up the Nile Valley from areas further south, but may also be due in part to the tropical hot conditions present at the site, even during glacial periods. The Jebel Sahaba sample are distinct in body shape from penecontemporary humans from Afalou-Bou-Rhumel (Algeria) and El Wad Natufians from the southern Levant—a result consistent with the results of both Irish (2000, 2005) using dental data and Franciscus (1995, 2003) using nasal data.

## Acknowledgements

Thanks to three anonymous reviewers who provided insightful comments on an earlier version of this manuscript. This research was supported in part by NSF (#SBR-9321339) and the LSB Leakey Foundation.

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