

# Behavioral inferences from the Skhul/Qafzeh early modern human hand remains

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Communicated by Erik Trinkaus, Washington University, St. Louis, MO, December 12, 2000 (received for review October 4, 2000)

Two groups of humans are found in the Near East  $\approx$ 100,000 years ago, the late archaic Neanderthals and the early modern Skhul/Qafzeh humans. Observations that Neanderthals were more heavily muscled, had stronger upper-limb bones, and possessed unusual shapes and orientations of some upper-limb joint complexes relative to the Skhul/Qafzeh hominids, have led some researchers to conclude that significant between-group upper-limb-related behavioral differences must have been present, despite the association of the two groups with similar Middle Paleolithic archeological complexes. A three-dimensional morphometric analysis of the hand remains of the Skhul/Qafzeh hominids, Neanderthals, early and late Upper Paleolithic humans, and Holocene humans supports the dichotomy. The Skhul/Qafzeh carpometacarpal remains do not have any unique morphologies relative to the other fossil samples remains examined. However, in the functionally significant metacarpal 1 and 3 bases they resemble Upper Paleolithic humans, not Neanderthals. Furthermore, the Skhul/Qafzeh sample differs significantly from the Neanderthals in many other aspects of hand functional anatomy. Given the correlations between changes in tool technologies and functional adaptations seen in the hands of Upper Paleolithic humans, it is concluded that the Skhul/Qafzeh hand remains were adapted to Upper Paleolithic-like manipulative repertoires. These results support the inference of significant behavioral differences between Neanderthals and the Skhul/Qafzeh hominids and indicate that a significant shift in human manipulative behaviors was associated with the earliest stages of the emergence of modern humans.

The Near Eastern human fossil and archeological records present a unique paleoanthropological situation because two morphologically distinct but archeologically very similar human groups, the late archaic Neanderthals and the early modern Skhul/Qafzeh hominids, existed at approximately the same time. Near Eastern Neanderthals are known from a number of 50,000- to 120,000-year-old sites in Israel, Syria, and Iraq (1–4). Neanderthals were craniofacially distinct, highly active, and comparatively very muscular. The fossil remains from the  $\approx$ 80,000- to 100,000-year-old site of Skhul (5) and the  $\approx$ 100,000-year-old site of Qafzeh (1, 2), both in Israel, are craniofacially more modern and less muscular than Neanderthals. Both groups are associated with Middle Paleolithic archeological complexes (6–9), indicating they used typologically and technologically similar toolkits for their subsistence activities.

Functional analyses of their skeletal remains demonstrate that the Skhul/Qafzeh sample had reduced upper-limb muscularity, reduced mechanical advantages in the hand, and reduced resistance to bending forces in the upper arm compared with the Neanderthals (10–16). These hominids appear to have used less somatic effort to accomplish upper-limb-related subsistence tasks than did the Neanderthals. Thus far, the anatomical evidence supports the hypothesis of significant behavioral contrasts between these two Near Eastern hominid groups, even though there is currently no archeological evidence supporting upper-limb-related behavioral distinctions (12, 13, 17). Our understanding of late Pleistocene human biocultural evolution will continue to be significantly hampered until these paradoxical lines of evidence are resolved.

This research on hand functional anatomy was undertaken to elucidate further the nature of the morphological and functional affinities of the Skhul/Qafzeh carpometacarpal (CMC) remains relative to Neanderthal, Upper Paleolithic early modern, and recent Holocene human samples. The orientations and shapes of the CMC articulations are adaptations to the levels and trajectories of forces produced during manipulation, and between-sample differences in CMC functional anatomy are informative of frequency shifts in habitual manipulatory behaviors (18, 19). Because the Skhul/Qafzeh sample is the earliest well-dated and reasonably complete sample of early modern humans known, elucidation of both their manual anatomy and upper-limb-related behavioral repertoires may have profound implications for the evolution of human manipulative behaviors associated with the emergence of behaviorally modern humans.

## Neanderthal and Upper Paleolithic Human Hand Functional Anatomy

Many researchers (e.g., refs. 20–25) have argued that the Neanderthals had limited manipulative capabilities. This idea was based largely on the mistaken belief that Neanderthals had relatively short thumbs, unusual thumb muscle morphology, and limited thumb mobility compared with recent humans. It is now clear that the Neanderthals had manipulative capabilities similar to those of modern humans, even though their hand remains have combinations of features that are at or beyond the range of recent human morphological variation (3, 18, 19, 26, 27). These include osteological indications of unusually hypertrophied hand musculature, significantly increased mechanical advantages across many joints, unusually broad fingertips, and unusual shapes and orientations of some of their CMC joints.

The first three features indicate that the Neanderthal hand was adapted primarily for greater grip strength during opposition and flexion of the thumb, cupping of the palm, and many wrist and hand movements relative to recent humans. All of these features contribute to the production of power grips, those in which objects are held in the palm of the hand with the thumb serving as a brace, implying that the Neanderthal manipulatory repertoire habitually required greater power compared with late Pleistocene early modern human manipulative repertoires. This is not to say that the Neanderthals did not, or could not, use precision grips, those in which the tip of the thumb is brought into contact with the pads of the fingers, inasmuch as there are no morphological indications of limited joint movements (3, 10, 18, 19, 26, 28).

More importantly, Neanderthals may have engaged in significantly altered frequencies of upper-limb behaviors relative to ethnohistorically documented hunter-gatherers, because mounting evidence from upper-limb articular morphology (including

Abbreviations: CMC, carpometacarpal; MC, metacarpal; EUP, early Upper Paleolithic; LUP, late Upper Paleolithic.

See commentary on page 2953.

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their CMC joints) indicates that the Neanderthals habitually loaded their joints not only at higher levels of joint reaction force, but also in different distributions of articular positions during peak loading (3, 14, 18, 19, 23, 28–31). Within the CMC region, the Neanderthal metacarpal (MC) 1 base tends to be dorsopalmarly flat to convex, lacking the prominent palmar beak typical of most recent human MC 1 bases. The Neanderthal morphology is probably an adaptation to the transmission of large axial loads (3). Compared with recent humans, the Neanderthal mid-CMC region is not as well adapted for resisting oblique joint reaction forces. Neanderthals have capitate-to-MC 2 and capitate-to-MC 3 articulations that tend to have reduced MC 3 styloid process projection and parasagittally rather than obliquely oriented MC 2 capitate facets (18, 19, 26). Despite archeological evidence for occasional hafting of Neanderthal-associated Middle Paleolithic tools (32–35), the above suite of features indicates that the Neanderthals probably did not use hafted tools that required the habitual use of oblique power grips. It may well be that an emphasis on woodworking, either with hand-held stone flakes or with flakes hafted into the distal rather than lateral aspects of handles, which were then held transversely across the palm of the hand, could account for many unique aspects of Neanderthal hand functional anatomy.

Interestingly, some early Upper Paleolithic (EUP) early modern human CMC functional complexes are morphologically and functionally intermediate between Neanderthal and recent Holocene human samples. Of special note is the fact that EUP and Neanderthal thumb CMC articulations are similar; both tend to have dorsopalmarly flat rather than concave MC 1 bases, although marginally greater development of the palmar beak is evident in EUP humans. Evidently, EUP humans and Neanderthals shared manipulatory behaviors that produced roughly similar levels of axial loads at the base of the thumb. However, both late Upper Paleolithic (LUP) and recent human MC1 bases are almost invariably dorsopalmarly concave, indicating reduced load levels at the base of the thumb.

Relative to Neanderthals, both EUP and LUP MC 3 bases have increased concavity of the facet for the MC 2 base, permitting enhanced pronation of the MC 2. This enhanced pronation is accompanied by slightly increased proximal projection of the MC 3 styloid process, but not to the extreme degree found in recent human samples. Additionally, whereas the Neanderthal MC 2 base is adapted for the transmission of primarily axially directed joint reaction forces, EUP MC 2 and 3 bases (given increased projection of their styloid process) are both adapted for increased oblique loads. These adaptations are more apparent in LUP specimens and are fully developed in recent human samples. Despite the presence of intermediate articular configurations, there are significant reductions in mechanical advantages on both the radial and ulnar sides of the hand of both EUP and LUP humans compared with Neanderthals when hamulus and trapezium tubercle projections are used to estimate muscle moment arms. Additionally, neither EUP nor LUP specimens have Neanderthal-like broad fingertips (19, 36).

In sum, when compared with the Neanderthals, the changes in EUP and LUP hand functional complexes often involved subtle alterations in joint shapes and orientations, whereas changes in joint mechanical advantages were more dramatic. The cumulative effects are increased stabilization of the mid-CMC region, the enhancement of first finger precision movements, and reductions in muscularity and mechanical advantages, all of which follow closely on the European Middle-to-Upper Paleolithic technological transition that began  $\approx 40,000$  B.P. The previously mentioned adaptive changes in the MC2/3 bases that stabilize the mid-CMC region are likely related to gradual increases in the frequency and sophistication of hafted tools used during the Upper Paleolithic, whereas functional adaptations related to more frequent precision grip usage, such as enhanced MC 2

pronation, are probably related to finer finger movements required for the engraving and incising of bone and antler artifacts.

Given this robust pattern of associated morphological and technological/behavioral evolution, the research question is therefore to determine where the Skhul/Qafzeh sample fits into this morphological continuum. The analysis is designed to test whether traditionally defined stone tool complexes are associated with specific CMC morphologies. Given their combined association with Middle Paleolithic lithic assemblages, the Skhul/Qafzeh hominids and Neanderthals should be most similar to each other. Such a result would weaken the hypothesis of between-sample behavioral distinctions. Alternatively, a finding that the Skhul/Qafzeh hominids are non-Neanderthal-like would lend further support to the behavioral distinction hypothesis.

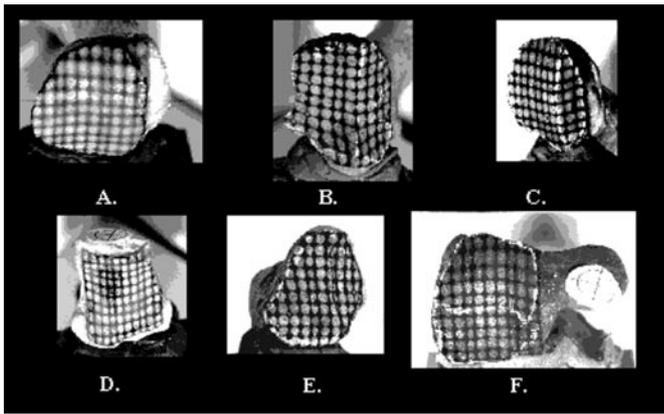
## Materials

The trapezia, capitates, hamates, and MCs 1, 3, and 5 from late Pleistocene and recent Holocene humans are used in this analysis. The primary concern for including specific skeletal elements is the presence of well-preserved, undistorted, and osteoarthritis-free articular facets. Data were collected on most of the available original late Pleistocene fossil hand remains. High-quality resin casts were used when original specimens were unavailable. The fossil specimens are divided into four samples: Neanderthals from Europe and the Near East, early and late Upper Paleolithic humans, and the Skhul/Qafzeh hominids. The Neanderthal sample consists of six European and seven Near Eastern individuals. Not all hand skeletons are complete; the sample size for each analysis varies from five to eight. The Upper Paleolithic specimens are associated with “nontransitional” industries, i.e., Aurignacian, Gravettian, Magdalenian, Epigravettian, and Kebaran. The sample is subdivided into the EUP (before 20,000 years ago) and LUP (after 20,000 years ago). The EUP sample consists of 12 individuals, and the LUP sample has nine. The actual number of specimens in each analysis varies from three to eight; the average EUP sample size is six, and the average LUP sample size is five. The Skhul/Qafzeh sample consists of Skhul 5 and Qafzeh 3, 7, 8, and 9. This sample has the least complete hand skeletons, so only 1–2 individuals are included in each analysis. All fossil specimens except the EUP-associated Arene Candide 1, an approximately 15-year-old male (37), are skeletally mature.

Comparative data also were collected on three Holocene human samples to maximize between-sample differences in articular size, population activity level, and indicators of hand muscularity. These were subsequently pooled into recent males ( $n = 15–19$ ) and females ( $n = 15–18$ ) for the analysis. The North American Urban sample, representing a relatively sedentary mid-20th century population, was taken from an autopsied skeletal collection of primarily European individuals. The late prehistoric Amerindian sample, A.D.  $\approx 1,250$  to 1,600, consists of individuals from Pueblo IV sites located in New Mexico’s central Rio Grande Valley. They have moderate levels of humeral and MC robusticity and upper-limb and hand muscularity (14, 18). The Mistihalj sample is from a Yugoslavian Medieval cemetery. These individuals exhibit rugose muscle markings and have large joint surfaces. Sexes were recorded from osteological inventory forms and rechecked by standard pelvic and cranial sexing techniques (38–40). Recent human male/female ratios are approximately equal, and given the potential systematic bias in between-sample differences in joint morphology introduced by functional adaptations to handedness, equal numbers of right and left sides are used.

## Methods

The raw data are three-dimensional landmark coordinates of the MC 1, 3, and 5 bases and the MC facets on the trapezium,



**Fig. 1.** Examples of grids projected on various recent human MC 1, 3, and 5 bases (A–C) and trapezium, capitate, and hamate MC facets (D–F). The landmarks are the digitized gridline intersections.

capitate, and hamate. Landmark coordinate data were acquired with photogrammetry, the extraction of three-dimensional information from digitized photographs. First, a  $10 \times 10$  grid that covers the maximum radioulnar and dorsopalmar extents of the facet is projected on each articular surface with a slide projector (Fig. 1). The specimen is then photographed from three or more angles with a calibrated 35-mm camera with a 1:1 90-mm macro lens, and the film negatives are scanned for use in a computer photogrammetry program, PHOTOMODELER (41). After the gridline intersections (the landmarks) are digitized on each image, the program calculates each landmark's three-dimensional coordinates to  $\pm 0.023$  mm.

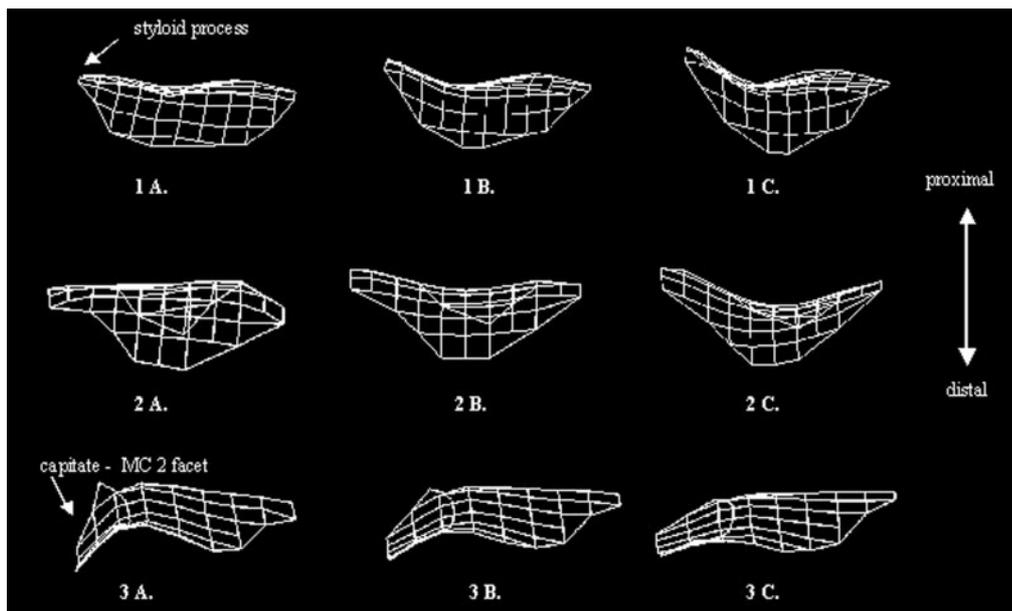
Landmark coordinates are used in the MORPHOLOGIKA computer software program (42). It first performs a separate Procrustes superimposition of the combined sample landmark coordinates for each MC base or carpal facet, fixing all objects to the same centroid size (size = 1). It fixes the objects without

changing the shapes, so it fixes only isometric shape differences (43, 44). This step is followed by separate principal components analysis of Kendall's tangent space coordinates (45), which summarizes the total sample shape variance for each MC base or carpal facet. Shape variation associated with the principal components is visualized in the program by "morphing" the three-dimensional rendered wire frame of the Procrustes mean MC base or carpal facet shape (Fig. 2).

Specimens are next assigned an *a priori* class (i.e., Neanderthal, EUP, LUP, or recent human male or female), and their principal components scores derived from the Morphologika program are used to produce a separate canonical discriminant function for each MC base or carpal facet with SAS statistical software (46). Only those functions with significant discriminations ( $P \leq 0.05$ ) are discussed in the results. The Skhul/Qafzeh specimens are inserted into the discriminant functions as unknowns and assigned to the nearest class based on the discriminant function Mahalanobis distance matrix. The results are indicative of morphological resemblance, and they form the basis for the functional and behavioral inferences discussed later.

## Results

The discriminant function classification results are presented in Table 1 and Fig. 3, and the posterior probabilities of membership in the *a priori* classes are listed in Table 2. Qafzeh 9's hamate-MC4/5 facets are morphologically most similar to the recent human female sample. The Qafzeh 9 MC 5 base and the capitate-MC 2/3 facets have high probabilities (0.70 and 0.85) of belonging to the Neanderthal sample, whereas the trapezium facet on the MC 1 base and the matching facet on the trapezium, plus the MC 3 base, are all classified as EUP or LUP with probabilities of 0.28,  $>0.99$ , and 0.92, respectively. The Qafzeh 3 capitate is placed in the Neanderthal sample with a relatively high probability of 0.71. The remaining specimens are classified as EUP (Qafzeh 3's hamate and Qafzeh 8's MC 3 base) or LUP (Skhul 5's MC 1 base and Qafzeh 7's trapezium) with moderate to high probabilities of 0.41, 0.77, 0.71, and 0.42.



**Fig. 2.** Examples of wire frames of the CMC facets visualized with the MORPHOLOGIKA software. The range of shape variation along some of the principal components (PC) of shape that contribute significantly to discriminating Neanderthals from recent humans is illustrated in the morphing of the combined sample Procrustes mean facet shapes: the MC 3 base (1A–1C), the MC 1 base (2A–2C), and the distal capitate facets (3A–3C). Neanderthals tend to have less styloid projection, flat to convex MC 1 bases, and more parasagittally oriented capitate MC 2 facets.

**Table 1. Classification results for the Skhul/Qafzeh specimens**

Carpal/metacarpal	As Neanderthal	As early Upper Paleolithic	As late Upper Paleolithic	As recent male or female
MC 1 base			Skhul 5, Qafzeh 9	
MC 3 base		Qafzeh 8, 9		
MC 5 base	Qafzeh 9			
Trapezium		Qafzeh 9	Qafzeh 7	
Capitate	Qafzeh 3, 9			
Hamate		Qafzeh 3		Qafzeh 9

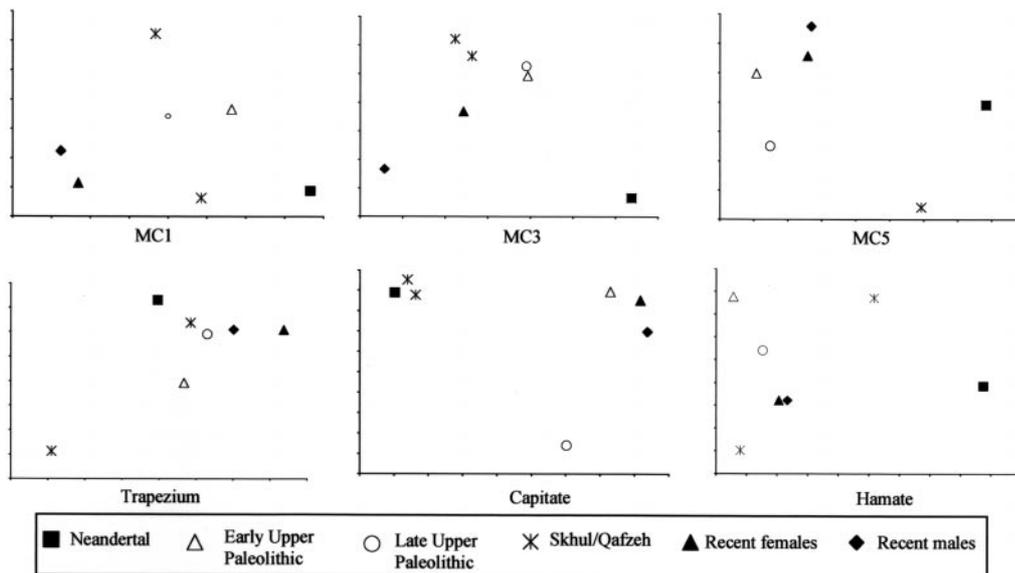
**Discussion**

Given their geological age, it is not surprising that the Skhul/Qafzeh CMC remains are most often assigned to one of the late Pleistocene fossil samples rather than the recent human sample. The most complete specimen, Qafzeh 9, bears morphological affinities to Neanderthals, EUP, LUP, or recent humans, depending on the CMC articulation in question. However, not all between-sample CMC morphological contrasts are equally distinctive, nor do all articular complexes have equal functional significance. The regions with the greatest between-sample discriminatory power, the MC 1, MC 2, and MC 3 bases (18, 19), are also functionally important complexes. Two of these regions were examined in this analysis. All Skhul/Qafzeh MC 1 and MC 3 bases are most similar to either the EUP or LUP sample morphologies, indicating UP-like levels of increased resistance to oblique joint reaction forces and enhanced MC 2 pronation. Thus, although of interest, less weight must be attributed to the result that the Qafzeh 3 and 9 capitate-MC 2/3 facets and the Qafzeh 9 MC 5 bases are classified as Neanderthal-like. Clearly, with the prominent exception of the Skhul/Qafzeh sample, between-sample contrasts in functionally relevant CMC morphological patterns are associated with traditionally defined lithic assemblages. One is therefore forced to conclude from this one exception that either between-sample differences in hand functional complexes are not informative of habitual behavioral repertoires, or the standard lithic typological categories are capable of discerning large-scale behavioral shifts but are sometimes inadequate for identifying more subtle, yet significant,

differences in behavior. This analysis indicates that the latter is more likely than the former.

Additional consideration must be given to the fact that the functional anatomy of the rest of the Skhul/Qafzeh hand remains are more similar to Upper Paleolithic rather than Neanderthal samples. For example, the Skhul/Qafzeh sample, like both EUP and LUP samples, has reduced muscle mechanical advantages at the base of the thumb and on the ulnar and radial sides of the wrist, relative to Neanderthals. Other significant similarities with EUP and LUP samples that contrast with Neanderthals include reductions in the development of muscle crests and fingertip widths (19). These features, plus the results just presented, demonstrate that the Skhul/Qafzeh and Neanderthal samples are distinct from each other in the most functionally significant regions of the hand and that the Skhul/Qafzeh hand remains are morphologically and functionally within the range of the combined EUP/LUP samples.

A recent review of the Middle Paleolithic to Upper Paleolithic archeological transition in Europe emphasizes the complex nature of the behavioral and technological transition (47). Nevertheless, the significant correlations between the evolution of the hand and the technological and behavioral changes occurring during the Upper Paleolithic of Europe cannot be ignored. These correlations indicate that hand functional anatomy may be used as a primary indicator of frequency shifts in habitual manipulatory repertoires, because habitual activities affect local rates of bone modeling and remodeling (48, 49). Because the Skhul/Qafzeh hands are morphologically and func-



**Fig. 3.** Plots of the CMC facet canonical discriminant functions. The class means are plotted on the first two canonical axes for the MC 1 base, MC 3 base, MC 5 base, and the trapezium, capitate, and hamate MC facets.

**Table 2. Posterior probabilities of membership in classes for Skhul/Qafzeh specimens**

	As Neanderthal	As early Upper Paleolithic	As late Upper Paleolithic	As recent male	As recent female
MC 1 base					
Skhul 5	0.01	0.19	0.71	0.05	0.04
Qafzeh 9	0.25	0.15	0.28	0.10	0.22
MC 3 base					
Qafzeh 8	<0.01	0.77	0.15	0.02	0.06
Qafzeh 9	<0.01	0.92	0.01	0.01	0.06
MC 5 base					
Qafzeh 9	0.70	0.08	0.15	0.01	0.06
Trapezium					
Qafzeh 7	0.17	0.02	0.42	0.39	0.02
Qafzeh 9	<0.01	>0.99	<0.01	<0.01	<0.01
Capitate					
Qafzeh 3	0.71	0.17	0.08	0.02	0.02
Qafzeh 9	0.85	0.05	0.05	0.02	0.03
Hamate					
Qafzeh 3	<0.01	0.40	0.41	0.04	0.06
Qafzeh 9	<0.01	<0.01	0.20	0.25	0.55

tionally like Upper Paleolithic samples, one must logically conclude that the Skhul/Qafzeh hominids habitually engaged in significantly more Upper Paleolithic-like rather than Neanderthal-like upper limb behaviors, regardless of the archeological evidence to the contrary.

The apparent equivalence of the Skhul/Qafzeh and Neanderthal associated lithic assemblages may be a function of the use of traditional typological methodologies, which, as made clear by the recent attempt of Shea (50) to document behavioral variability among the Levantine Neanderthal and Skhul/Qafzeh groups, cannot always discern subtle behavioral variation. Given the patterns of between-sample morphological and functional similarities discovered in this analysis, the Skhul/Qafzeh homi-

nids were most likely using oblique grips and finer finger movements more frequently than were the Neanderthals. Notably, the skeletal evidence presented here, in the context of late Pleistocene patterns of modern human emergence, indicates that significant shifts in habitual manipulative behavior were associated with the early emergence of modern humans. Such behavioral shifts may well have been one of the primary components of the subsequent spread of early modern humans.

I thank the numerous curators for their generosity in granting access to the collections and fossil specimens used in this research. Data collection and analysis were supported by grants from the L. S. B. Leakey Foundation, the National Science Foundation, and the University of New Mexico.

- Grün, R. & Stringer, C. B. (1991) *Archaeometry* **33**, 153–199.
- Valladas, H., Joron, J.-L., Valladas, G., Arensburg, B., Bar-Yosef, O., Belfer-Cohen, A., Goldberg, P., Laville, H., Meignen, L., Rak, Y., et al. (1987) *Nature (London)* **330**, 159–160.
- Trinkaus, E. (1983) *The Shanidar Neanderthals* (Academic, New York).
- Trinkaus, E. (1991) *L'Anthropol. (Paris)* **95**, 535–572.
- McDermott, F., Grün, R., Stringer, C. B. & Hawkesworth, C. J. (1993) *Nature (London)* **363**, 252–255.
- Mercier, N. H., Valladas, J.-L., Bar-Yosef, O., Vandermeersch, B., Stringer, C. & Joron, J.-L. (1993) *J. Archeol. Sci.* **20**, 169–174.
- Mercier, N. & Valladas, H. (1994) in *Late Quaternary Chronology and Paleoclimates of the Eastern Mediterranean*, eds Bar-Yosef, O. & Kra, R. (Univ. of Arizona Department of Geosciences, Tucson), pp. 12–20.
- Schwarz, H. (1994) in *Late Quaternary Chronology and Paleoclimates of the Eastern Mediterranean*, eds Bar-Yosef, O. & Kra, R. (Univ. of Arizona Department of Geosciences, Tucson), pp. 33–54.
- Schwarz, H. P. R., Grün, R., Vandermeersch, B., Bar-Yosef, O., Valladas, H. & Tchernov, E. (1988) *J. Hum. Evol.* **7**, 619–636.
- Trinkaus, E. (1983) in *The Mousterian Legacy: Human Biocultural Change in the Upper Pleistocene*, ed. Trinkaus, E., British Archaeological Reports S164 (Archaeopress, Oxford), pp. 165–200.
- Trinkaus, E. (1992) in *The Evolution and Dispersal of Modern Humans in Asia*, ed. Akazawa, T. (Univ. of Tokyo Press, Tokyo), pp. 277–294.
- Trinkaus, E. (1995) *Paléorient* **21**, 9–23.
- Trinkaus, E. & Churchill, S. (1999) *J. Archeol. Sci.* **26**, 173–184.
- Churchill, S. E. (1994) *Human Upper Body Evolution in the Eurasian Later Pleistocene* (Univ. of New Mexico, Albuquerque).
- Vandermeersch, B. (1981) *Les Hommes Fossiles de Qafzeh (Israel)* (Centre National de la Recherche Scientifique, Paris).
- Churchill, S. E., Pearson, O. M., Grine, F. E., Trinkaus, E. & Holliday, T. W. (1996) *J. Hum. Evol.* **31**, 213–237.
- Trinkaus, E., Ruff, C. B. & Churchill, S. E. (1998) in *Neanderthals and Modern Humans in West Asia*, eds Akazawa, T., Aoki, K. & Bar-Yosef, O. (Plenum, New York), pp. 391–404.
- Niewoehner, W. A., Weaver, A. & Trinkaus, E. (1997) *Am. J. Phys. Anthropol.* **103**, 219–233.
- Niewoehner, W. A. (2000) *The Functional Anatomy of Late Pleistocene and Recent Human Carpometacarpal and Metacarpophalangeal Articulations* (Univ. of New Mexico, Albuquerque).
- Bonch-Osmolovskij, G. A. (1941) *Paleolit Kryma* **2**, 1–172.
- Boule, M. (1913) *L'Homme Fossile de la Chapelle-aux-Saints* (Masson, Paris).
- Sarasin, F. (1932) *Z. Morphol. Anthropol.* **30**, 252–316.
- Musgrave, J. H. (1971) *Nature (London)* **233**, 538–541.
- Vlček, E. (1975) *Bull. Mem. Soc. Anthropol. Paris Sér. XIII* **2**, 257–276.
- Vlček, E. (1978) *Morphol. Cong. Symp. Charles Univ. (Prague)* **19**, 89–99.
- Trinkaus, E. & Villemeur, I. (1991) *Am. J. Phys. Anthropol.* **84**, 249–260.
- Villemeur, I. (1991) *La Main des Néandertaliens* (Centre National de la Recherche Scientifique, Paris).
- Trinkaus, E., Churchill, S. E., Villemeur, I., Riley, K. G., Heller, J. A. & Ruff, C. B. (1991) *J. Anthrop. Soc. Nippon* **99**, 257–278.
- Churchill, S. E. & Trinkaus, E. (1990) *Am. J. Phys. Anthropol.* **83**, 147–160.
- Trinkaus, E. & Churchill, S. (1988) *Am. J. Phys. Anthropol.* **75**, 15–21.
- Hambücker, A. (1993) *C. R. Acad. Sci. Paris* **317**, 109–114.
- Boëda, E., Connan, J., Dessort, D., Muhesen, S., Mercier, N., Valladas, H. & Tisnérat, N. (1996) *Nature (London)* **380**, 336–338.
- Shea, J. J. (1989) in *The Human Revolution*, eds Mellars, P. & Stringer, C. (Princeton Univ. Press, Princeton), pp. 611–625.
- Beyries, S. (1988) in *Upper Pleistocene Prehistory of Western Asia*, eds Dibble, H. L. & Montet-White, A. (Univ. of Pennsylvania, Philadelphia), pp. 213–223.
- Anderson-Gerfaud, P. (1990) in *The Emergence of Modern Humans*, ed. Mellars, P. (Edinburgh Univ. Press, Edinburgh), pp. 389–418.
- Musgrave, J. H. (1973) in *Human Evolution*, ed. Day, M. H. (Taylor and Francis, London), pp. 59–85.
- Sergi, S., Parenti, R. & Paoli, G. (1974) *Mem. Istit. It. Paleontol. Umana* **2**, 13–38.
- Olivier, G. (1969) *Practical Anthropology* (Thomas, Springfield, IL).
- Phenice, T. (1969) *Am. J. Phys. Anthropol.* **30**, 297–301.

40. Steele, D. G. & Bramblett, C. (1988) *The Anatomy and Biology of the Human Skeleton* (Texas A&M Univ. Press, College Station).
41. Eos Systems (1993) PHOTOMODELER Software (Eos Systems, Vancouver).
42. O'Higgins, P. & Jones, N. (1998) MORPHOLOGIKA Software (University College, London).
43. Dryden, I. L. & Mardia, K. V. (1993) *Sankya* **55**, 460–480.
44. Dryden, I. L. & Mardia, K. V. (1998) *Statistical Shape Analysis* (Wiley, London).
45. Kendall, D. G. (1984) *Bull. London Math. Soc.* **16**, 81–121.
46. SAS (1989) SAS Software (SAS, Carey, NC).
47. d'Errico, F., Zilhão, J., Julien, M., Baffier, D. & Pelegrin, J. (1998) *Curr. Anthropol.* **39S**, S1–S44.
48. Frost, M. H. (1979) *Calcif. Tissue Int.* **28**, 181–200.
49. Frost, M. H., Ferretti, J. & Jee, W. (1998) *Calcif. Tissue Int.* **62**, 1–7.
50. Shea, J. J. (1998) *Curr. Anthropol.* **39**, S45–S78.