



A 3D quantitative comparison of trapezium and trapezoid relative articular and nonarticular surface areas in modern humans and great apes

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Abstract

The structure and functions of the modern human hand are critical components of what distinguishes *Homo sapiens* from the great apes (*Gorilla*, *Pan*, and *Pongo*). In this study, attention is focused on the trapezium and trapezoid, the two most lateral bones of the distal carpal row, in the four extant hominid genera, representing the first time they have been quantified and analyzed together as a morphological-functional complex. Our objective is to quantify the relative articular and nonarticular surface areas of these two bones and to test whether modern humans exhibit significant shape differences from the great apes, as predicted by previous qualitative analyses and the functional demands of differing manipulative and locomotor strategies. Modern humans were predicted to show larger relative first metacarpal and scaphoid surfaces on the trapezium because of the regular recruitment of the thumb during manipulative behaviors; alternatively, great apes were predicted to show larger relative second metacarpal and scaphoid surfaces on the trapezoid because of the functional demands on the hands during locomotor behaviors. Modern humans were also expected to exhibit larger relative mutual joint surfaces between the trapezoid and adjacent carpals than do the great apes because of assumed transverse loads generated by the functional demands of the modern human power grip. Using 3D bone models acquired through laser digitizing, the relative articular and nonarticular areas on each bone are quantified and compared. Multivariate analyses of these data clearly distinguish modern humans from the great apes. In total, the observed differences between modern humans and the great apes support morphological predictions based on the fact that this region of the human wrist is no longer involved in weight-bearing during locomotor behavior and is instead recruited solely for manipulative behaviors. The results provide the beginnings of a 3D comparative standard

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against which further extant and fossil primate wrist bones can be compared within the contexts of manipulative and locomotor behaviors.

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Introduction

The bones of the wrist, as a morphological and functional unit, play an important role in connecting the thumb and fingers with the forearm, while facilitating a variety of movements and force distributions. The primate wrist is involved in performing various functions, which can generally be classified as relating to positional and manipulative behaviors. Of the extant hominids,¹ only *Homo sapiens* does not habitually use the hands for locomotion. Instead human hands are used primarily as organs of manipulation. Great ape hands, however, are regularly involved in both locomotion and manipulation. The African apes (*Gorilla*, *Pan*) often engage in arboreal, suspensory behaviors, but are predominantly terrestrial knuckle-walking quadrupeds (Tuttle, 1967, 1969a; Tuttle and Watts, 1985; Hunt, 1992; Remis, 1995, 1998; Doran, 1996). The orangutan (*Pongo*) is almost exclusively arboreal; the principal locomotor behavior of *Pongo* is typically described as arboreal quadrumanulism, because of the similar ways in which the hands and feet are used (Sugardjito, 1982; Sugardjito and van Hooff, 1986; Cant, 1987; Rose, 1988). When on the ground, *Pongo* exhibits a variety of hand postures, including knuckle-walking and palmigrady, but in general, a complete or modified version of fist-walking is observed (Tuttle, 1967, 1975; Tuttle and Beck, 1972; Susman, 1974).

The kinds of manipulative behavior and the ways in which they are performed are quite variable among the great apes. While the hands are used regularly for daily events such as feeding, grooming, and nesting in all the great apes, only chimpanzees

and orangutans have been observed habitually using tools for feeding (sensu McGrew and Marchant, 1997) in the wild (McGrew, 1992; van Schaik et al., 1996, 2003; Whiten et al., 1999). In contrast, over the course of hominin evolution, the hand has become free of the demands of locomotor behavior, such that, in modern humans, it is recruited extensively for tool-using and tool-making behaviors, having tremendous capability in this regard.

Investigating how the morphological structures of the hand, and particularly the wrist, relate to function and ultimately behavior presents many challenges. In particular, researchers must often decide between using a qualitative or quantitative approach in their analyses of the wrist. During the past century, the subtle yet complex nature of wrist morphology has been qualitatively described in detail by several authors (e.g., Napier, 1955a,b, 1956, 1960, 1961, 1962, 1966; Marzke, 1971, 1983, 1992, 1997; Lewis, 1977, 1989; Sarmiento, 1985, 1988; Whitehead, 1993). These studies speak to the variety of potential functional and phylogenetic information contained within the carpus and surrounding soft tissue anatomy. However, a weakness of qualitative descriptions and analyses is that the nature of the underlying continuous variation in the morphology being studied remains obscure. Without more information about the distribution of features within a given sample, it is difficult to objectively evaluate and interpret similarities or differences in morphology.

Quantitative approaches, particularly those that incorporate multivariate statistical analyses, attempt to ameliorate the difficulties involved in qualitative data analysis. These approaches are extremely important in trying to obtain objective knowledge of the patterns of wrist variation observed both intra- and interspecifically (Conroy and Fleagle, 1972; Zwell and Conroy, 1973;

¹ Hominid is used here to indicate membership in the family Hominidae, including *Homo*, *Pan*, *Gorilla*, and *Pongo* (Darga et al., 1972; Begun, 2002).

Corruccini et al., 1975; Corruccini, 1978; McHenry, 1983; Tocheri et al., 2003). In attempts to quantify wrist anatomy, the use of multivariate statistical techniques is often necessary given the complex sets of features present on each bone (e.g., multiple joint surfaces, ligament and muscle attachments, bony tubercles). Nonetheless, selecting quantitative data that reasonably represent the complex morphology is anything but straightforward, as different data sets may produce inconsistent results (Conroy and Fleagle, 1972; Zwell and Conroy, 1973; Corruccini et al., 1975, 1976). Lewis (1989: 170), in light of such inconsistencies, argued: “That such a supposedly objective technique should lead to such divergent results might be thought surprising: what these results really demonstrate are the limitations of multivariate methods particularly when applied to a complex area such as the wrist where there are formidable difficulties in formulating metrical data which adequately reflect the morphology.”

Three-dimensional (3D) methods and analyses, which focus on 3D landmark, surface, and/or volume data, represent a logical approach to quantifying complex morphology. An added benefit is that 3D approaches can retain many of the observational and comparative strengths of qualitative research through enhanced visualization techniques. Therefore, it is possible to quantify the expression of features that more adequately reflect the true morphology and its underlying distribution, while maintaining the ability to evaluate the results in the context of previous morphological observations and descriptions.

In this study, we focus on the trapezium and trapezoid, the two most lateral bones of the distal carpal row, and their respective articular and nonarticular surfaces (Figs. 1–4). Traditionally, the carpometacarpal joint of the thumb has received the most attention in both anthropological and clinical studies because of its importance in studying manipulative behavior (e.g., Haines, 1944; Napier, 1955a; Tuttle, 1969b; Kuczynski, 1974; Cooney and Chao, 1977; Trinkaus, 1989; Rose, 1992). The scaphoid-trapezium-trapezoid (STT) region of the wrist has also become an important focus in some recent clinical studies (Kauer, 1986; Moritomo et al., 2000a,b; Sonenblum et al., 2004).

The complex shapes of the trapezium and trapezoid and their respective joint surfaces make this a difficult region to analyze quantitatively; however, using 3D techniques presently available, many of these difficulties can be overcome and new insights into the comparative and functional morphology of this region of the wrist may be revealed.

Research objectives

This study represents the first time all of the articular and nonarticular areas of the trapezium and trapezoid have been quantitatively analyzed together. Observed similarities and differences in relative surface areas between extant genera should provide important information regarding the functional morphology of these two carpal elements in hominids. The analyses presented herein quantitatively test previous morphological descriptions of the trapezium and trapezoid. For instance, the first metacarpal joint surface on the trapezium is often described as being broader and flatter, particularly dorsopalmarly, in modern humans compared to the great apes (Lewis, 1977, 1989; Susman and Creel, 1979; Trinkaus, 1989; Marzke, 1997). The scaphoid joint surfaces on the trapezium and trapezoid have also been described as different in relative size between humans and great apes (Marzke et al., 1992). Specifically, Marzke et al. (1992) observed that modern humans display a larger scaphoid surface on the trapezium relative to the scaphoid surface on the trapezoid, while the great apes and other primates, including *Hylobates* and *Papio*, display the opposite condition. If this difference is related to function, then the first and second metacarpal surfaces of the trapezium and trapezoid, respectively, may also show differences in relative size that correlate with the surfaces for the scaphoid.

Further differences between modern humans and the great apes were qualitatively described by Lewis (1989). He suggested that the modern human trapezoid has altered from the primitive primate condition such that it facilitates the modern human power grip by enabling the transmission of forces transversely across the palmar aspect of the wrist rather than strictly in an axial direction. His

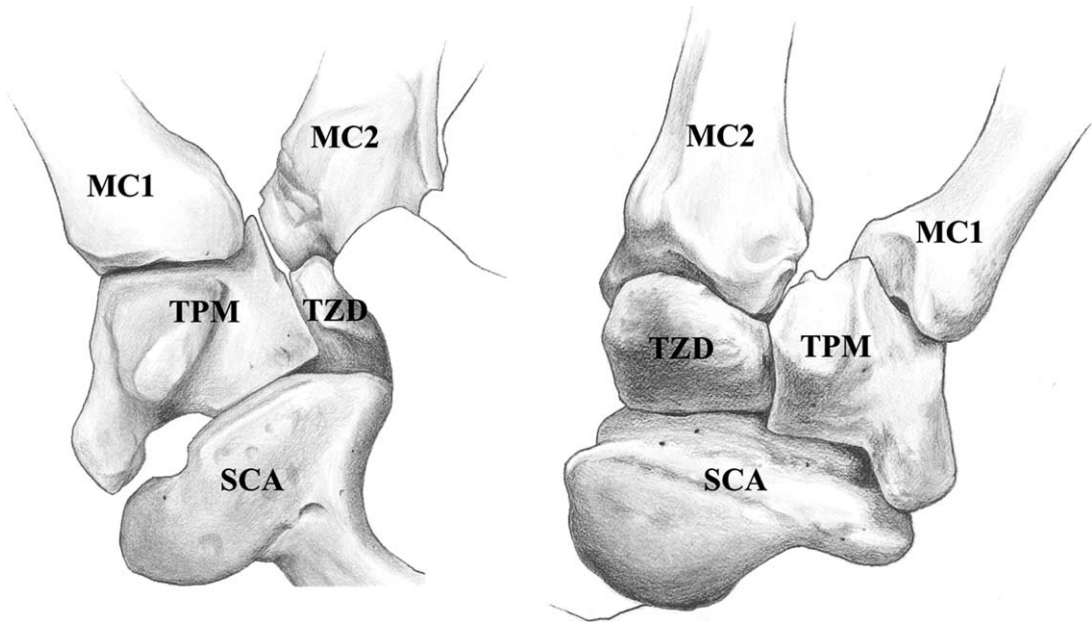


Fig. 1. Illustration of the bones and joints of the lateral hominid wrist; the left side of a gorilla is shown in palmar (left) and dorsal (right) views (TPM = trapezium, TZD = trapezoid, SCA = scaphoid, MC1 = first metacarpal, and MC2 = second metacarpal).

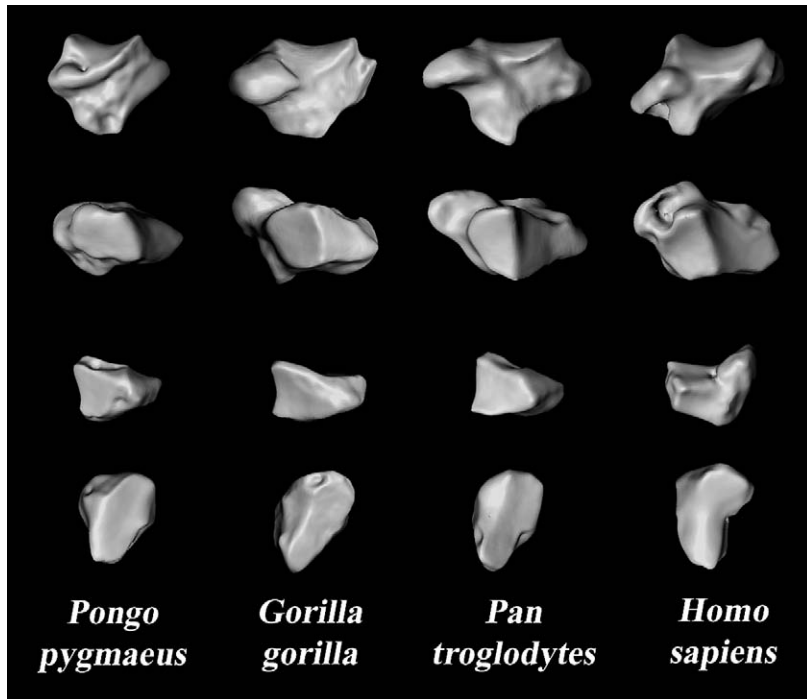


Fig. 2. Examples of the 3D models of hominid trapezia and trapezoids that were used for this study. Note the well-defined articular and nonarticular surface topography, which is the result of the high resolution of the laser digitizer used to acquire these data. The trapezia are shown in mediopalmar (top) and proximal (second from top) views; the trapezoids are shown in proximal (second from bottom) and distal (bottom) views.

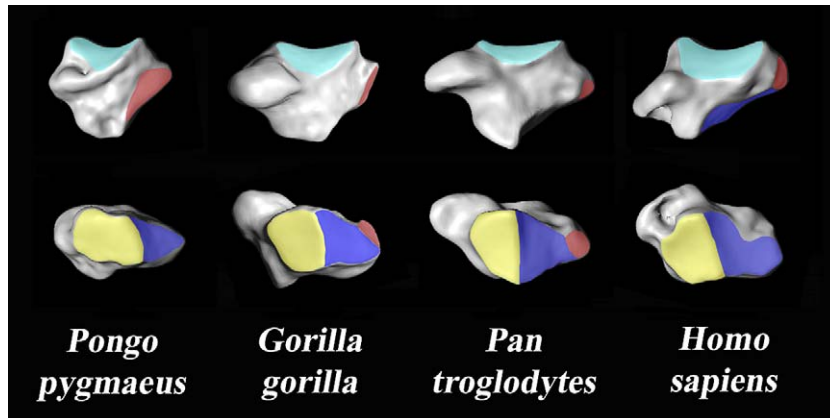


Fig. 3. Three-dimensional models of hominid trapezia with segmented articular areas shown in mediopalmar (top) and proximal (bottom) views (teal = first metacarpal, red = second metacarpal, blue = trapezoid, yellow = scaphoid/os centrale).

interpretations predict that modern humans should exhibit larger relative trapezoid area on the trapezium and larger relative trapezium, capitate, and nonarticular (due to a broadening of the palmar portion) areas on the trapezoid than do the great apes.

Our main objective in this study is to objectively quantify the articular and nonarticular surface areas of the trapezium and trapezoid in an effort to discern patterns of morphological variation that distinguish modern humans from the great apes. The exploratory hypothesis is that modern humans should exhibit a morphological pattern that is different from that of great apes due to the

difference in emphasis on manipulative vs. locomotor behaviors. In general, there is increased recruitment of the thumb during manipulative behaviors in modern humans compared with the load-bearing requirements of great ape locomotor behaviors. The exploratory hypothesis predicts that: 1) modern humans will have relatively larger first metacarpal and scaphoid surfaces on the trapezium, while the great apes will have relatively larger second metacarpal and scaphoid surfaces on the trapezoid; and 2) modern humans will have relatively larger capitate, trapezium, and non-articular surfaces on the trapezoid, as well as a relatively larger trapezoid surface on the

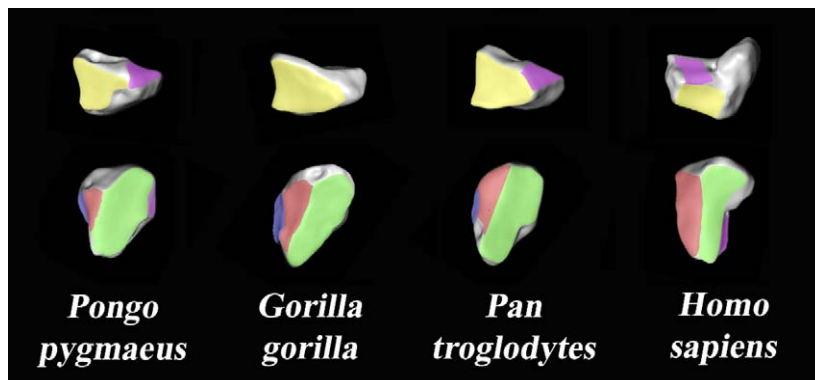


Fig. 4. Three-dimensional models of hominid trapezoids with segmented articular areas shown in proximal (top) and distal (bottom) views (red = lateral second metacarpal, green = medial second metacarpal, purple = capitate, blue = trapezoid, yellow = scaphoid).

trapezium, than do the great apes. Such patterns, if present, may be useful for generating more specific hypotheses about functional and behavioral correlates of wrist morphology in extant hominids and also for interpreting hand and wrist function in extinct hominids. In sum, we bring the knowledge of this region from previous studies together with present 3D computation and visualization techniques to enable a comprehensive, detailed analysis of trapezium and trapezoid surface area morphology.

Materials and methods

Using 3D techniques, we quantified the articular and nonarticular surface areas, as well as total bone surface area, on the trapezium and trapezoid of 108 individuals. The sample includes specimens from the Cleveland Museum of Natural History (Hamann-Todd Osteological Collection), the Smithsonian's National Museum of Natural History, the Royal Ontario Museum, and the Department of Anthropology, Arizona State University. The bones come from 18 *Pongo pygmaeus* (11 male, 7 female), 30 *Gorilla gorilla* (15 male, 15 female), 30 *Pan troglodytes* (15 male, 15 female), and 30 modern *Homo sapiens* (15 male, 15 female). The methods used are similar to those described previously (Tocheri et al., 2003), and thus are only briefly outlined here.

Three-dimensional models of each bone were acquired by laser scanning using the portable Cyberware Model 15 laser digitizer and accompanying modeling software (see <http://www.cyberware.com>). Each model consists of approximately 1100 points per square centimeter resulting in a data set of x, y, and z values known as a 3D point cloud. Each point cloud was triangulated enabling the surface to be modeled topologically. All articular surfaces were segmented from the triangular mesh using a watershed-based hybrid segmentation scheme for triangular meshes (Mangan and Whitaker, 1999; Pulla, 2001; Razdan et al., 2002; Razdan and Bae, 2003; Tocheri et al., 2003). The segmentation procedure involved calculating the absolute curvature value at each vertex and

estimating local regions of similar curvature. Absolute curvatures represent the sum of the absolute values of the principal curvatures, k_{\min} and k_{\max} , at each vertex (Farin and Hansford, 2000; Pulla, 2001). In general, segmenting is comparatively straightforward because the vertices along the joint boundaries typically have larger absolute curvature values relative to vertices on either side of the boundaries (Fig. 5). The surface area of each triangle in the mesh was computed by taking the cross product of any two edges, or vectors, that span each triangle and dividing by two (Farin and Hansford, 2000); region surface areas were then computed by summing over all the triangles in each desired region (see Figs. 3 and 4).

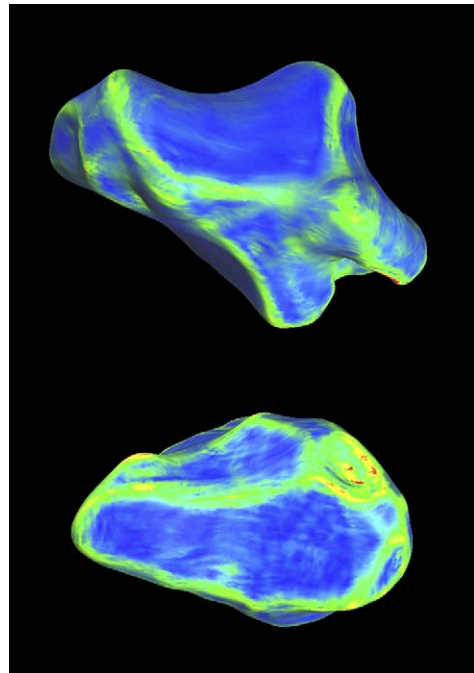


Fig. 5. Curvature map showing local regions with relative lower (in blue) and higher (in green) absolute curvature values. Note that articular boundaries tend to have higher relative absolute curvature values than articular surfaces, thus facilitating the articular surfaces to be segmented with repeated accuracy. Human trapezium (top) in mediopalmar view and gorilla trapezoid (bottom) in distal view are shown.

Size adjustment

One of the primary goals of this analysis was to emphasize biomechanical features of the trapezium and trapezoid that may be important in locomotor and/or manipulative behaviors. In that sense, we did not want to simply remove the effects of size; rather, we wanted to remove the effects of scale. In order to compare the articular and nonarticular areas of these differently sized hominid genera, shape ratios were calculated by dividing each area by the total surface area of the bone on which it is located. These ratios represent scale-free shape variables (Mosimann and James, 1979; Jungers et al., 1995) and enable the examination of whether significant differences in shape exist between taxa. Moreover, using total bone surface area as the denominator simplifies interpretation, since an area divided by an area results in a percentage. In other words, the result is the percentage (%) of total bone surface area that is represented by each specific joint surface or nonarticular region. In this study, total trapezium surface area was used as the denominator for all examined trapezium regions and total trapezoid surface area was used for all trapezoid regions. Whether the shape differences analyzed in this study are correlated with overall body size is an important empirical question requiring further investigation, but is beyond the scope of the present study.

Statistical analyses

We used discriminant analysis (DA) to explore whether the relative surface areas of the trapezium and trapezoid are effective in discriminating modern humans from the great apes. Discriminant analysis is a multivariate technique that allows several variables to be examined simultaneously in multidimensional space. The DA generates a linear combination of the variables for estimating the posterior probability of belonging to a genus given a set of trapezium and trapezoid data values. The posterior probability therefore represents the likelihood of correctly assigning an individual to its respective genus based on 3D surface area data collected from the trapezium and trapezoid. The

cross-validation method was used to calculate the posterior probability of membership in each genus given a set of relative surface areas because it gives approximately unbiased estimates of the probabilities of misclassification (Johnson and Wichern, 2002).

A total of three DAs were performed: one each for data from the trapezium and trapezoid and one that included data from both. N-dimensional patterns in these data were also reduced to three canonical variables. These three variables were interpreted using the pooled-within canonical structure, which represents the correlations between pairs of linear combinations of the variables for each genus and each canonical variable. Plotting these canonical variables enables the observed differences between genera to be examined and interpreted graphically (Johnson and Wichern, 2002).

In order to better interpret the multivariate results and, in particular, to help convey which relative surface areas are the best discriminators between modern humans and the great apes, 95% confidence limits for each relative surface area were generated using the simple percentile bootstrap method (Efron and Tibshirani, 1993; Manly, 1997), in which the confidence interval is the middle 95% of the bootstrap distribution (based on $B = 1000$ bootstrap samples). Although normality tests for the raw data did not suggest any significant departures from a normal distribution, the bootstrap results ensure that statements about differences between the means can be made with statistical confidence ($p \leq 0.05$).

Results

For each DA, the cross-validated posterior probabilities are summarized in Table 1a, b, c while plots of the two largest canonical scores show the divergences among the four genera in each analysis (Figs. 6–8). The relative surface areas that best account for the distribution along the canonical axes are evident from the correlations with each axis. All variables and eigenvalues have statistically significant F -statistic values ($p < 0.0001$). The means and 95% confidence

Table 1a

Cross-validated posterior probabilities of misclassification using the relative articular and nonarticular areas of the trapezium

	<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>
<i>Homo</i>	24	5	1	0
%	80.0	16.7	3.3	0.0
<i>Pan</i>	5	19	6	0
%	16.7	63.3	20.0	0.0
<i>Gorilla</i>	1	3	22	1
%	3.3	20.0	73.3	3.3
<i>Pongo</i>	1	0	3	14
%	5.6	0.0	16.7	77.8

Table 1b

Cross-validated posterior probabilities of misclassification using the relative articular and nonarticular areas of the trapezoid

	<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>
<i>Homo</i>	29	1	0	0
%	96.7	3.3	0.0	0.0
<i>Pan</i>	0	21	1	8
%	0.0	70.0	3.3	26.7
<i>Gorilla</i>	0	1	28	1
%	0.0	3.3	93.3	3.3
<i>Pongo</i>	1	7	0	10
%	5.6	38.9	0.0	55.6

Table 1c

Cross-validated posterior probabilities of misclassification using the relative articular and nonarticular areas of the trapezium and trapezoid

	<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>
<i>Homo</i>	30	0	0	0
%	100.0	0.0	0.0	0.0
<i>Pan</i>	0	30	0	0
%	0.0	100.0	0.0	0.0
<i>Gorilla</i>	0	1	28	1
%	0.0	3.3	93.3	3.3
<i>Pongo</i>	0	2	0	16
%	0.0	11.1	0.0	88.9

limits of each relative surface area are summarized in Table 2 and Figs. 9–13. Comparisons of the relative surface areas within and between the trapezium and trapezoid reveal several significant differences between these hominid genera. In this paper, we focus solely on the observed differences between modern humans and the great apes. The differences among the great apes will be discussed elsewhere.

DA-1: Relative surface areas of the trapezium (Fig. 6)

The first canonical axis (CAN1) accounts for 66% of the variation. Both chimpanzees and gorillas cluster in the middle of this axis, whereas orangutans are more toward the right (+) and humans cluster more toward the left (-). The correlations with CAN1 indicate that this axis represents a comparison of the second metacarpal surface (0.7) with the first metacarpal (-0.4) and trapezoid (-0.5) surfaces. This clustering pattern is the result of orangutans having a larger relative second metacarpal surface (Fig. 9) and humans having larger relative first metacarpal (Fig. 10a) and trapezoid (Fig. 11) surfaces. Chimpanzees cluster closer to humans because of a larger relative trapezoid surface than in gorillas and orangutans.

The second canonical axis (CAN2) accounts for 29% of the variation. Humans and orangutans cluster together on this axis above the cluster of chimpanzees and gorillas. The correlations with CAN2 indicate that the observed variation is accounted for by a comparison of the nonarticular area (-0.9) with all four articular areas (0.4–0.8). This clustering pattern is the result of humans and orangutans having less relative trapezium nonarticular area than the African apes (Fig. 12).

The cross-validation procedure resulted in the correct classification of 22 gorillas (73.3%), 24 humans (80%), 19 chimpanzees (63.3%), and 14 orangutans (77.8%) (Table 1a). These results suggest that the relative surface areas of the trapezium are reasonable discriminators of extant hominids at the genus level, particularly for *Homo* and *Pongo*.

DA-2: Relative surface areas of the trapezoid (Fig. 7)

CAN1 accounts for 76% of the variation. Chimpanzees and orangutans cluster in the middle of this axis, whereas humans cluster to the left (-) and gorillas to the right (+). The correlations with CAN1 indicate that this axis represents a comparison of the capitate surface (-0.8) with the scaphoid

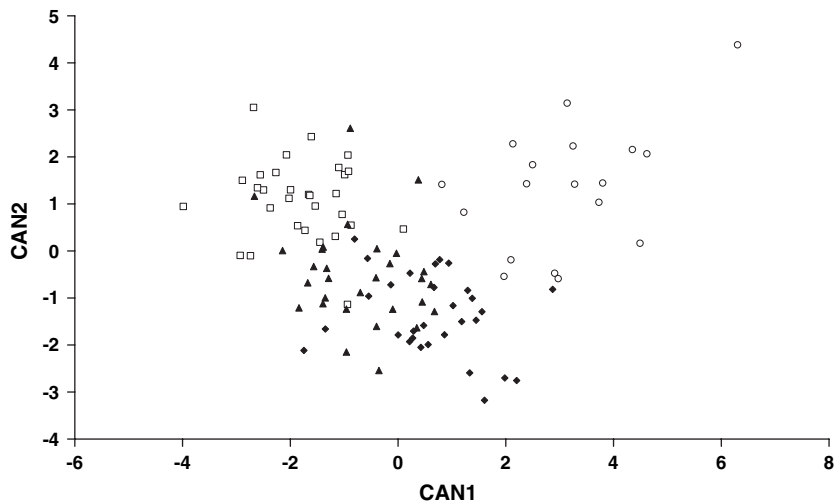


Fig. 6. Plot of the canonical variables (CAN1, CAN2) generated from analysis of the relative surface areas of the trapezium (*Homo* = open squares, *Pan* = solid triangles, *Gorilla* = solid diamonds, *Pongo* = open circles).

(0.6) and medial² second metacarpal (0.4) surfaces. This clustering pattern is the result of gorillas having a small, or nonexistent, capitate surface,³ and humans having a larger relative capitate (Fig. 11) and smaller relative medial second metacarpal (Fig. 10b) and scaphoid (Fig. 13) surfaces.

CAN2 accounts for 22% of the variation. Chimpanzees and orangutans cluster together on

² The second metacarpal surface on the trapezoid is typically V-shaped and is easily subdivided into medial and lateral portions (Figs. 4 and 5). Therefore, in the multivariate analysis, the medial and lateral portions of this articulation are analyzed separately.

³ In gorillas, the dorsomedial aspect of the trapezoid typically has either a very small articulation or none at all for the capitate (Fig. 4) (Broom and Schepers, 1946; Le Gros Clark, 1947; McHenry, 1983; Lewis, 1989). The lack of a trapezoid–capitate articulation in the gorilla contributes to the proportionately larger nonarticular area on the trapezoid compared with chimpanzees and orangutans. Modern humans also have significantly larger trapezoid nonarticular area; however, the scaphoid surface is proportionately smaller and the non-articular area is relatively larger on the palmar and dorsomedial aspects of the bone in comparison to the great apes (Fig. 4). Complete diarthroidal capitate surfaces can occur on gorilla trapezoids (McHenry, 1983; Lewis, 1989; this study), but overall, the severely reduced or absent joint is the most frequent condition in gorillas and is likely derived from the more common primitive condition observed in primates (Lewis, 1989).

this axis, situated above the cluster of humans and gorillas. The correlations with CAN2 indicate that the observed variation is accounted for by a comparison of the nonarticular area (−0.8) with the scaphoid (0.6) and capitate (0.4) surfaces. This clustering pattern is the result of humans and gorillas having larger relative nonarticular areas (Fig. 12) and, again, different sized capitate surfaces (Fig. 11).

The cross-validation procedure resulted in the correct classification of 28 gorillas (93.3%), 29 humans (96.7%), 21 chimpanzees (70.0%), and 10 orangutans (55.6%) (Table 1b). These results suggest that the relative surface areas of the trapezoid are reasonable discriminators of extant hominids at the genus level, particularly for *Gorilla* and *Homo*.

DA-3: Relative surface areas of the trapezium and trapezoid (Fig. 8)

CAN1 accounts for 67% of the variation. The correlations with CAN1 indicate that this axis represents a comparison of surface areas from both bones. Those with the strongest correlations with this axis include the first metacarpal (0.4) and nonarticular (−0.4) surfaces of the trapezium and the scaphoid (−0.5), medial second metacarpal

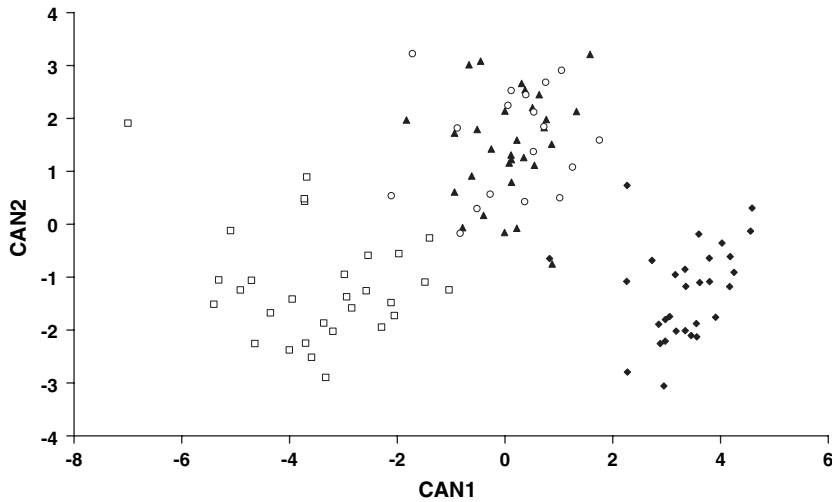


Fig. 7. Plot of the canonical variables (CAN1, CAN2) generated from analysis of the relative surface areas of the trapezoid (*Homo* = open squares, *Pan* = solid triangles, *Gorilla* = solid diamonds, *Pongo* = open circles).

(−0.3), and capitate (0.6) surfaces of the trapezoid. The clustering of each genus along this axis is accounted for by similar reasons as stated above for DA-1 and DA-2.

CAN2 accounts for 22% of the variation. The correlations with CAN2 also indicate that the observed variation is accounted for by a comparison of surface areas from both bones. The second metacarpal surface (0.7) on the trapezium and the

nonarticular (−0.4) and capitate (0.5) surfaces on the trapezoid show the strongest correlations with this axis. This axis separates orangutans from African apes and humans because of the larger relative trapezium–second metacarpal surface in orangutans (Fig. 9).

The cross-validation procedure resulted in the correct classification of 28 gorillas (93.3%), all humans (100%) and chimpanzees (100%), and 16

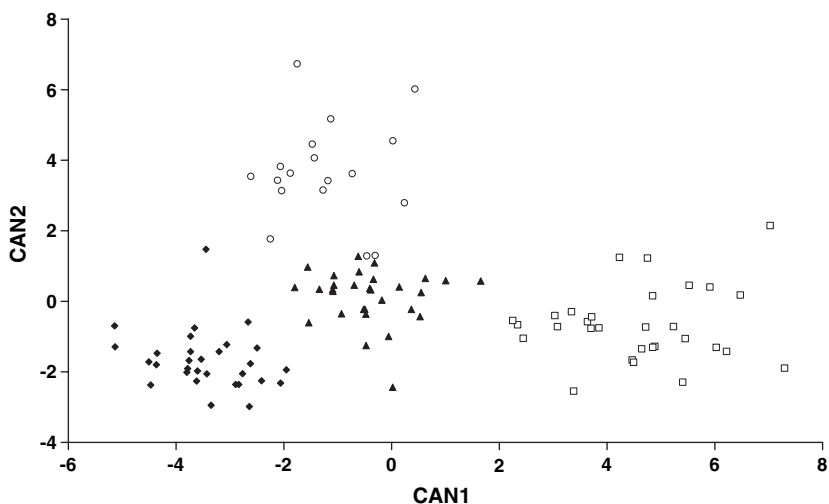


Fig. 8. Plot of the canonical variables (CAN1, CAN2) generated from analysis of the relative surface areas of the trapezium and trapezoid (*Homo* = open squares, *Pan* = solid triangles, *Gorilla* = solid diamonds, *Pongo* = open circles).

Table 2
Relative trapezium and trapezoid surface area (%) means and 95% confidence limits of the means generated from 1000 bootstrapped samples^a

Genus	N	Relative surface areas on the trapezium						Relative surface areas on the trapezoid					
		MC1	MC2	TZD	SCA	NART	MC2	medial MC2	lateral MC2	TPM	SCA	CAP	NART
<i>Homo</i>	30	17.3	2.9	9.6	8.0	62.2	20.9	12.8	8.2	12.7	8.4	7.8	50.3
		16.8–18.0	2.7–3.2	9.3–9.9	7.6–8.3	61.3–63.1	20.1–21.7	12.2–13.4	7.6–8.7	12.3–13.2	7.7–9.0	7.0–8.7	49.1–51.4
<i>Pan</i>	30	14.1	2.7	9.2	6.3	67.7	23.5	16.2	7.2	13.3	14.6	5.3	43.4
		13.5–14.8	2.4–2.9	8.8–9.6	6.0–6.7	66.6–68.8	22.6–24.2	15.7–16.8	6.6–7.8	12.7–13.9	14.2–15.2	5.0–5.5	42.3–44.5
<i>Gorilla</i>	30	12.7	2.9	7.2	5.8	71.3	23.2	17.1	6.1	10.6	14.7	0.3	51.3
		12.2–13.3	2.7–3.2	6.7–7.6	5.4–6.3	70.3–72.4	22.4–23.9	16.5–17.7	5.6–6.7	10.1–11.1	14.2–15.2	0.0–0.7	50.3–52.3
<i>Pongo</i>	18	14.3	6.3	7.5	6.1	65.6	21.8	16.1	5.6	12.6	14.4	5.7	45.5
		13.7–15.0	5.7–6.9	7.0–7.9	5.2–7.1	63.9–67.3	20.9–22.7	15.2–17.0	4.9–6.4	11.7–13.6	13.5–15.3	5.3–6.2	43.8–47.2

^a MC1 = first metacarpal, MC2 = second metacarpal, TPM = trapezium, TZD = trapezoid, SCA = scaphoid, CAP = capitate, NART = nonarticular.

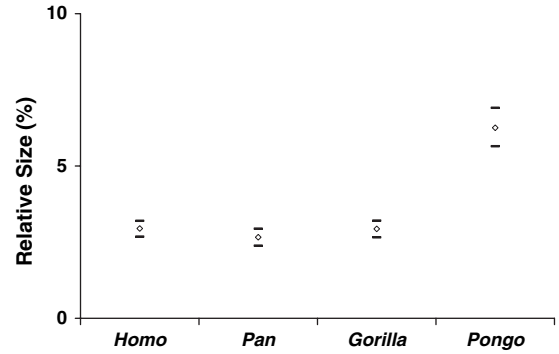


Fig. 9. Means and 95% confidence limits for the relative area of the second metacarpal surface on the trapezium (open diamonds). Note that *Pongo* shows a larger relative second metacarpal surface than the hominines.

orangutans (88.9%) (Table 1c). These results suggest that the relative surface areas of the trapezium and trapezoid, when examined together, are an excellent discriminator of all extant hominids at the genus level.

Performing the DA with orangutans or gorillas removed results in the same posterior probabilities of misclassification and clustering as above; removing humans results in one chimpanzee misclassified as a gorilla, whereas removing chimpanzees results in zero misclassifications. The consistency of these results indicates that the various combinations of relative surface areas described above have strong discriminatory power among these genera. It should also be emphasized that when genus clusters are examined by sex, the males and females of each genus appear randomly within each cluster. Therefore, within each genus there is little to no trapezium and trapezoid shape dimorphism despite the differences in body size between males and females in each taxon. Thus, the observed shape differences between genera may have functional, behavioral, and/or phylogenetic significance.

Discussion

The primary objective of this study was to explore whether modern humans exhibit differences from the great apes in the relative surface areas of the trapezium and trapezoid. The 3D

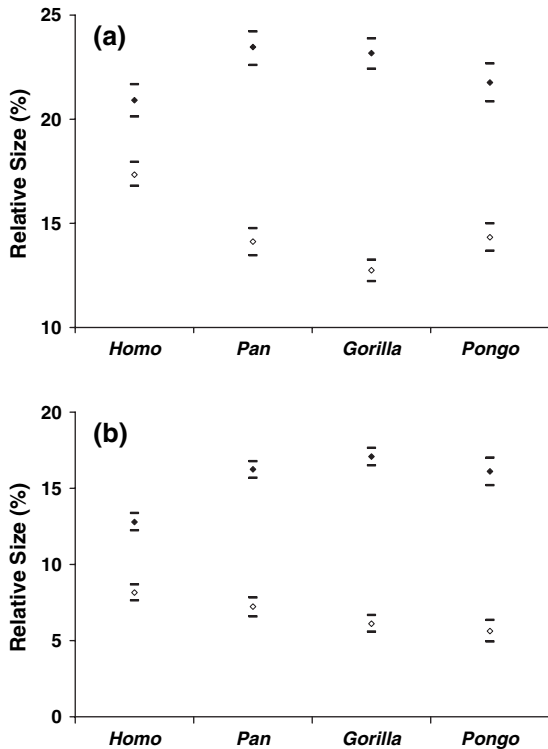


Fig. 10. a. Means and 95% confidence limits of the relative areas of the first metacarpal surface (open diamonds) on the trapezium and the second metacarpal surface (solid diamonds) on the trapezoid. Note that *Homo* shows a larger relative first metacarpal surface and a smaller relative second metacarpal surface than do the great apes. b. Means and 95% confidence limits for the relative areas of the lateral (open diamonds) and medial (solid diamonds) aspects of the second metacarpal surface on the trapezoid. Note that *Homo* shows a larger relative lateral surface and a smaller relative medial surface than do the great apes.

quantitative results of this study provide detailed information as to how the morphology of these two carpal bones differs between modern humans and the great apes. Modern humans have proportionately larger joint surfaces on the trapezium for the scaphoid and first metacarpal, whereas the great apes have proportionately larger surfaces on the trapezoid for the scaphoid and medial second metacarpal. The great apes have proportionately more nonarticular area on the trapezium, whereas humans have proportionately more on the trapezoid. Clearly, a combination of several relative surface areas on the modern human trapezium and

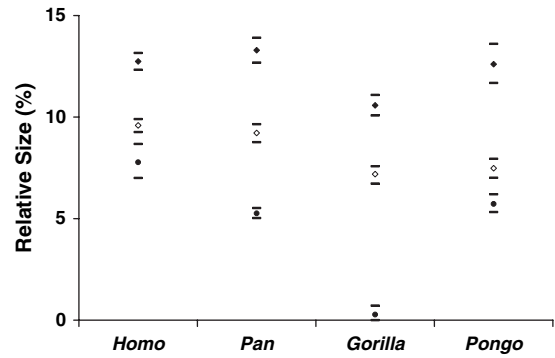


Fig. 11. Means and 95% confidence limits for the relative areas of the trapezoid surface on the trapezium (open diamonds), and the trapezium (solid diamonds) and capitata (solid circles) surfaces on the trapezoid. Note that *Homo* and *Pan* show a larger relative trapezoid surface than do *Gorilla* and *Pongo*, while *Homo* also shows a larger relative capitata surface than do the great apes.

trapezoid is distinctly different from those observed in great apes (Figs. 9–13).

These observed morphological patterns are consistent with basic differences between humans and great apes in thumb- and index-finger-use. In the great apes, compressive loads are transmitted through the second metacarpal–trapezoid–scaphoid and into the forearm during terrestrial locomotion (Jenkins and Fleagle, 1975; Sarmiento, 1988). Muscle contraction during suspensory locomotion also probably loads the bones in tension across

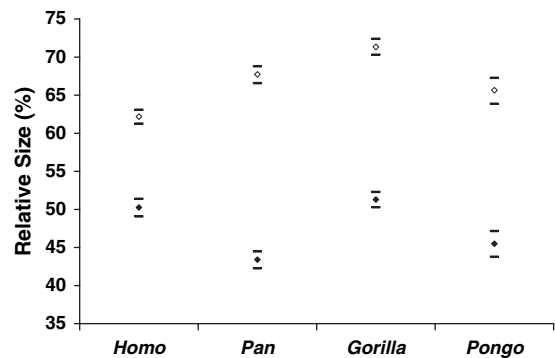


Fig. 12. Means and 95% empirical confidence limits for the relative areas of the nonarticular surfaces on the trapezium (open diamonds) and trapezoid (solid diamonds). Note that *Homo* and *Gorilla* show a larger relative trapezoid nonarticular area than do *Pan* and *Pongo*, while *Homo* also shows a smaller relative trapezium nonarticular area than do the great apes.

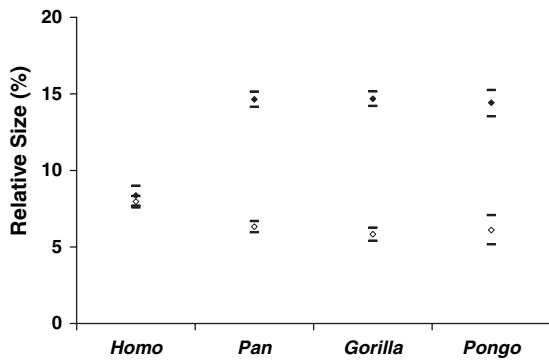


Fig. 13. Means and 95% confidence limits for the relative areas of the scaphoid surfaces on the trapezium (open diamonds) and the trapezoid (solid diamonds). Note that *Homo* shows a larger relative scaphoid surface on the trapezium and a smaller relative scaphoid surface on the trapezoid than do the great apes.

these joints. In contrast, human locomotion does not stress these joints; instead, forceful pinching and grasping of objects focus large forces on the joint between the first metacarpal and trapezium (Cooney and Chao, 1977; Momose et al., 1999; Bettinger et al., 1999, 2000), which are then transmitted to the scaphoid. These forces may be better accommodated by the proportionately large mutual joint surfaces on the trapezium for the first metacarpal and scaphoid. Visually the difference is apparent in the radioulnar broadening of the palmar aspect of the first metacarpal surface in humans (Figs. 3 and 5). This aspect undergoes contact with the first metacarpal during opposition of the thumb, virtually doubling the contact area compared to when the thumb is abducted palmarly or radially (Momose et al., 1999). The large contact area during opposition helps stabilize the joint, particularly during grips that utilize a strong pinch (Momose et al., 1999).

The first metacarpal surface of all four genera has a saddle configuration that permits movement of the metacarpal toward the fingers in opposition. The extent of curvature of the mutual first carpometacarpal surfaces may also affect the range of this movement (Marzke and Marzke, 2000). Thus, range of motion, in addition to load transmission, must be considered as a factor in the interpretation of the morphological differences

between modern humans and the great apes at this joint. Future analyses that include the mutual joint surface on the first metacarpal are necessary before more definitive statements can be made regarding potential differences affecting thumb ranges of motion.

Human manipulative behavior also generates large relative loads through the hand and wrist at the base of the index finger (Momose et al., 1999; Bettinger et al., 2000), and a distinct morphology appears to accommodate these loads. Articular facets on the proximal second metacarpal for the trapezium and for the capitate are more transversely oriented than in the great apes (Marzke, 1983, 1997; Tocheri et al., 2003). This configuration may allow for the distribution of load between the second metacarpal and these two distal wrist bones as well as to the trapezoid, but experimental results are needed to support such a claim. This distinct pattern of orientation of the three joints between the second metacarpal and the trapezium, trapezoid, and capitate allows for slight pronation of the metacarpal, providing some “give” in this region by enabling the index finger to pronate during hand clenching as well as strong lateral pinch and three-jaw chuck grips (Van Dam, 1934; Lewis, 1989; Marzke, 1997).

Several aspects of the quantitative evidence presented here support the interpretations of Lewis (1989) that the modern human trapezoid has changed from the condition in the great apes such that it may better distribute loads across the palmar aspect of the hand. Humans have a significantly larger relative surface area for the trapezoid on the trapezium and for the capitate on the trapezoid. The latter articulation is also more palmarly placed than in the great apes. The relative areas of the nonarticular regions on the trapezoid (concentrated on the palmar and dorsomedial aspects of the bone) are also significantly larger.

The increased amount of relative nonarticular area on the modern human trapezoid contributes to a blunt, roughly square bony area on the palmar aspect of the human trapezoid, located between the distal second metacarpal surface and the convergence of the scaphoid and trapezium surfaces proximally (Figs. 4 and 14). This morphology contributes to the relatively larger

capitate articulation located on the medial aspect of the trapezoid. The capitate articular surface is anterior to a transverse trapezoid–capitate ligament, which attaches to the relatively larger dorsomedial nonarticular area. In modern humans, the enlarged palmar nonarticular area of the trapezoid is the site of two ligament attachments (Fig. 14); the volar trapezium–trapezoid ligament attaches to the most anterior aspect, while the distolateral aspect (often referred to as the “zipper” of the boot in osteology texts) is the attachment area of a dorsal ligament that runs to the volar-ulnar tubercle of the trapezium, deep to the origin of the trapezium–capitate ligament (Bettinger et al., 1999, 2000; Bettinger and Berger, 2001). During pinch grips, cantilever bending forces are applied to the trapezium, requiring the bone and the first carpometacarpal joint to be stabilized (Bettinger et al., 2000). The volar and dorsal trapezium–trapezoid ligaments may play a role in stabilizing the trapezium and first carpometacarpal joint, in conjunction with other important stabilizing ligaments, such as the trapezium–third metacarpal and dorsoradial ligaments (Bettinger et al., 2000). The palmar nonarticular area of the modern human trapezoid also occasionally provides attachment of the deep head of the flexor pollicis brevis (Day and Napier, 1961; Jenkins, 1998) and the oblique head of the adductor pollicis muscles (Jenkins, 1998). Nonarticular

area on this portion of the great ape trapezoid is considerably smaller than in humans or totally absent, resulting in a more wedge-shaped appearance of the trapezoid rather than the characteristic boot-shape seen in modern humans (Figs. 2, 4, and 14).

In contrast to humans, the trapezoid–capitate joint is typically absent in gorillas (Fig. 4) (Broom and Schepers, 1946; Le Gros Clark, 1947; McHenry, 1983; Lewis, 1989), while in chimpanzees and orangutans it is located posteriorly, behind a massive interosseous ligament that joins the capitate and trapezoid, and becomes continuous with a ligament running transversely between the second and third metacarpals (Marzke, 1983; Lewis, 1989). The arrangement of the chimpanzee and orangutan diathrosis and ligament attachment is also characteristic of most other primates (Lewis, 1989). The dorsolateral region of the modern human capitate is beveled away, and accommodates the styloid process of the third metacarpal (Marzke and Marzke, 1987), as well as the relatively larger dorsomedial nonarticular area of the trapezoid. The human pattern, with the articulation in a position anterior to the midline trapezoid–capitate ligament, may transmit forces from the first carpometacarpal region across the broad palmar aspect of the trapezoid to the anterior capitate, which also appears broadened distally (Lewis, 1989).

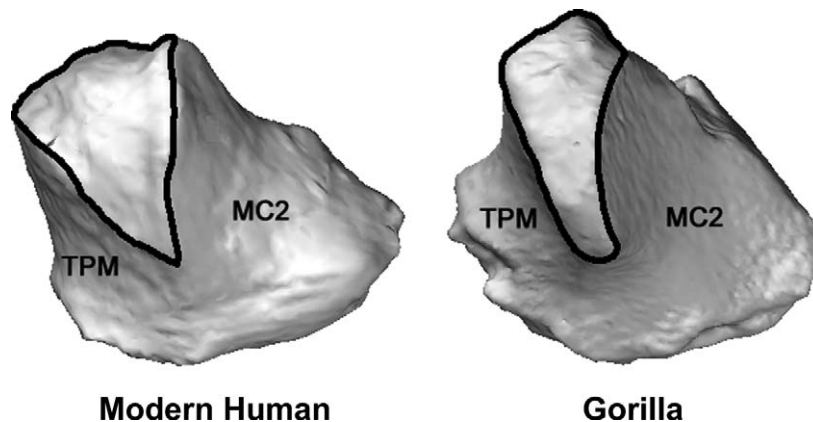


Fig. 14. Three-dimensional trapezoid models showing the basic difference in relative size and shape of the palmar trapezoid nonarticular area (outlined in black) between modern humans and great apes. Both bones are scaled to roughly the same size; the articular surfaces for the trapezium (TPM) and second metacarpal (MC2) are shown to indicate the orientation.

In total, the configuration observed in modern humans is consistent with a hypothesis of functional morphology that can accommodate proportionately larger loads through the trapezium and across the palmar aspect of the human wrist. It is only in modern humans that we observe a more palmar location of the trapezoid–capitate articulation, as well as radioulnar broadening of the palmar portions of the human trapezoid and capitate. Together, these features suggest that loads may be distributed transversely across the entire base of the palm. Power grips that involve the thenar and hypothenar pads coming together forcefully, and possibly strong precision pinch grips between the thumb and fingers, might be accommodated by this morphological pattern, which appears derived in modern humans among extant hominids. Biomechanical and kinetic analyses, however, are needed to further test these hypotheses, as well as the interpretations presented here.

Conclusions

The structure and functions of the modern human hand are critical components of what distinguishes modern humans from the great apes. Our 3D quantitative analysis of the articular and nonarticular surface areas of the trapezium and trapezoid has revealed several statistically significant morphological differences between modern humans and the great apes. Many of these differences were previously qualitatively described by various researchers, but this study represents the first time they have been quantified and analyzed together as a morphological-functional complex. The observed morphological differences between modern humans and the great apes support predictions based on the fact that this region of the human wrist is no longer involved in weight-bearing during locomotor behavior and is instead primarily recruited for participation in manipulative behaviors. The results provide the beginnings of a 3D comparative standard against which further extant and fossil hominid wrist bones can be compared within the contexts of manipulative and locomotor behaviors.

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